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PORTADA DE *Iberus*

Iberus gualterianus (Linnaeus, 1758), una especie emblemática de la península Ibérica, que da nombre a la revista. Dibujo realizado por Toza.

Iberus

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How many species of *Candidula* (Gastropoda: Hygromiidae) in northern Portugal?

¿Cuantas especies de *Candidula* (Gastropoda: Hygromiidae) habitan en el norte de Portugal?

Cristian R. ALTABA*

Recibido el 6-II-1996. Aceptado el 24-IV-1996

ABSTRACT

Two species of *Candidula* Kobelt, 1871 (Pulmonata: Hygromiidae) endemic to Portugal are reported from the northern part of the country. *C. belemensis* (Servain, 1880) is considered a valid species similar to, but different from the widespread *C. intersecta* (Poiret, 1801). *C. olisippensis* (Servain, 1880) is distinctive, having a shell with very small, round umbilicus, a long spermathecal duct, and a short flagellum.

RESUMEN

Se citan para el norte de Portugal dos especies endémicas en este país pertenecientes al género *Candidula* Kobelt, 1871 (Pulmonata: Hygromiidae). *C. belemensis* (Servain, 1880) es considerada como una especie válida similar, pero diferente, a la ampliamente distribuida*C. intersecta* (Poiret, 1801). *C. olisippensis* (Servain, 1880) es de fácil distinción, al tener una concha con un ombligo redondeado y pequeño, un largo conducto de la espermateca y un corto flagelo.

KEY WORDS: Gastropoda, Hygromiidae, *Candidula*, Portugal, distribution, taxonomy.
PALABRAS CLAVE: Gastropoda, Hygromiidae, *Candidula*, Portugal, distribución, taxonomía.

INTRODUCTION

The genus *Candidula* Kobelt, 1871 comprises several species of hygromiid land snails living in Western Europe. In the Iberian Peninsula this genus has undergone a remarkable diversification, particularly along the Atlantic drainages (ALTONAGA, GÓMEZ, MARTÍN, PRIETO, PUENTE AND RALLO, 1994). The taxonomy of this genus is complex because the diagnostic characters of the various species are not conspicuous, either in the internal anatomy or in the shells. The species of *Candidula* living in Portugal are still poorly known, yet this country has at least four endemics (ALTIMIRA, 1969; GITTENBERGER, 1985, 1993). This note is a contribution towards a revision of the genus in the Iberian Peninsula (Ondina and Altaba, *in prep.*).

Two little-known, apparently rare species of *Candidula* are reported here, collected during a field trip in April

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1994 in northern Portugal. These species were described by SERVAIN (1880), and subsequently ignored for over a century (NOBRE, 1930, 1941; SEIXAS, 1992). Conchological and anatomical data indicate that the species studied here are indeed distinct taxa. The specimens are kept in the author's malacological collection.

RESULTS

Family HYGROMIIDAE Tryon, 1866
Genus *Candidula* Kobelt, 1871

Candidula belemensis (Servain, 1880) (Figs. 1, 2)

C. belemensis was known up to date only from the original locality (Lisbon) and three other sites further south (GITTENBERGER, 1993). A single fresh shell was found at the base of the old city walls of Valença do Minho, at the northern border of Portugal (UTM 29T NG25; Figs. 1, 2). This locality represents a considerable extension of the species' known range. It is likely, however, that *C. belemensis* lives also further north, in Galicia, where specimens having a long flagellum have been reported as *C. intersecta* by CASTILLEJO (1986).

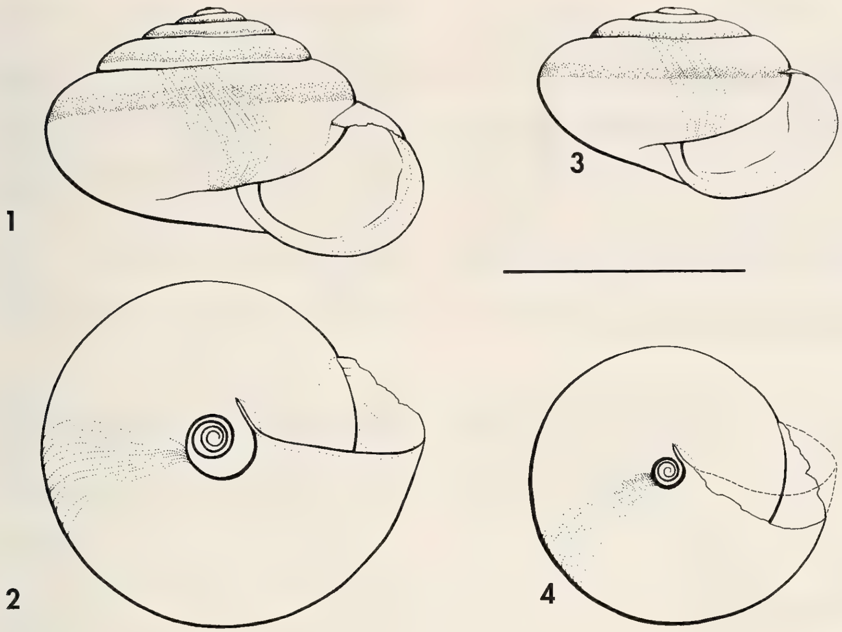
This species is probably closely related to *C. intersecta* (Poiret, 1801), which ranges discontinuously throughout Atlantic Europe, from southern Portugal to southern Sweden (KERNEY AND CAMERON, 1979; GITTENBERGER, 1993; ALTONAGA *et al.*, 1994). *C. belemensis* differs conchologically from the latter in having a more depressed shell with a broader aperture, a wide and slightly eccentric umbilicus, and a much shallower sculpture of radial ribs and minute spiral striae (GITTENBERGER, 1993).

Anatomically it differs from NW-European *C. intersecta* in the relatively longer flagellum, which is about half the length of the epiphallus (GITTENBERGER, 1993). However, populations of *C. intersecta* from NW-Iberia have a flagellum shorter than half the length of the epiphallus, as is typical of that species (MANGA GONZÁLEZ, 1979). Thus, the available evidence suggests that *C. belemensis* is not conspecific with co-occurring *C. intersecta*.

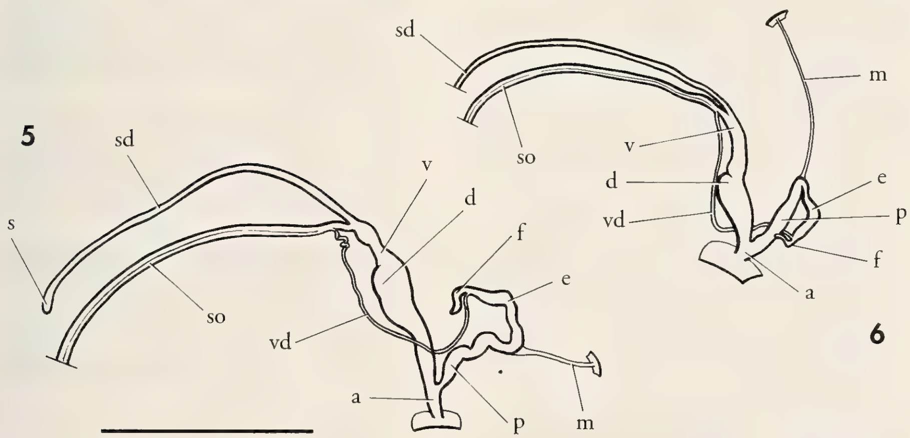
Candidula olisippensis (Servain, 1880) (Figs. 3-6)

Two subadult specimens were collected under bolders in the vicinity of the Sanctuary of Sameiro, near Braga (UTM 29T NF59; Figs. 3, 4). Although the aperture edge of their shells was still tender and became damaged, it bears a conspicuous whitish internal rib. The radulae have one central, and 22 and 24 lateral teeth. These numbers fall within the range of other *Candidula* species from northwestern Iberia (MANGA GONZÁLEZ, 1979).

The genitalia (still immature) of both specimens are shown in Figures 5 and 6. The flagellum is distinct, proximally narrow, and very short, measuring about 1/4 the length of the epiphallus, which is somewhat shorter and thinner than the penis. The bursa is small, oblong and indistinctly united to its duct, which lies appressed to the spermoviduct throughout and is exceedingly long, measuring almost twice the length of the penis and epiphallus combined. There are no glandulae mucosae, their location being occupied instead by a moderate swelling at the proximal end of the vagina. The dart sac appears partially developed, being only a large medial swelling of the vagina with no trace of a dart, but exhibiting two large internal longitudinal folds adjacent to two shallow invaginations, the lower one bordered by a few papillae. This internal structure can be interpreted as an immature stage of that described for other species of *Candidula*



Figures 1-4. Shells of *Candidula* from northern Portugal. 1, 2: *C. belemensis* from Valença do Minho (CRA 4895); 3, 4: *C. olisippensis* from Sameiro, near Braga (CRA 4866-1). Scale bar 5 mm.
Figuras 1-4. Conchas de Candidula *del norte de Portugal. 1, 2:* C. belemensis *de Valença do Minho (CRA 4895); 3, 4:* C. olisippensis *de Sameiro, cerca de Braga (CRA 4866-1). Escala 5 mm.*



Figures 5, 6. Proximal genitalia of two immature specimens of *Candidula olisippensis.*
Abbreviations. A: atrium; E: epiphallus; F: flagellum; M: penial retractor muscle; P: penis; S: bursa copulatrix; SD: duct of the bursa; SO: spermoviduct; V: vagina; VD: vas deferens. Scale bar 2 mm.
Figuras 5, 6. Genitalia proximal de dos especimenes inmaduros de Candidula olisippensis.
Abreviaturas. A: atrio; E: epifalo; F: flagelo; M: músculo retractor peneal; P: pene; S: bursa copulatrix; SD: conducto de la bursa; SO: espermoviducto; V: vagina; VD: vaso deferente. Escala 2 mm.

(HAUSDORF, 1988, 1991), confirming the generic assignation by GITTENBERGER (1993), who examined a dried specimen in poor condition.

Several nominal species described by LOCARD (1899) are probably synonyms of *Helix olisippensis* Servain 1880. The general shape of the shell in this species (or species complex) is fairly variable, yet it is always fairly thin, with rounded or slightly angular periphery, very narrow roundish umbilicus, spire formed by flattened whorls separated by an indented suture, radial sculpture moderately developed, and microspiral striae well marked (GITTENBERGER, 1993). *Candidula olisippensis* is apparently endemic to Portugal. The current finding represents the northern limit of its known range.

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Nuevos datos sobre la distribución de la superfamilia Helicoidea Rafinesque, 1815 (Gastropoda, Pulmonata, Stylommatophora) en el oeste de Galicia

New records about the distribution of the superfamily Helicoidea Rafinesque, 1815 (Gastropoda, Pulmonata, Stylommatophora) in the West of Galicia

Paz ONDINA, Jesús HERMIDA y Adolfo OUTEIRO*

Recibido el 21-IV-1996.Aceptado el 30-IV-1996

RESUMEN

En este trabajo se realiza un estudio faunístico de las especies de la superfamilia Helicoidea Rafinesque, 1815, encontradas en el oeste de Galicia (provincias de A Coruña y Pontevedra). Para cada especie se incluyen citas previas y localidades de captura con las coordenadas U.T.M. 10x10 km. Teniendo en cuenta nuestros hallazgos y los de los autores consultados en la bibliografía se han elaborado los mapas de distribución correspondientes, en sistema U.T.M. de 10x10 km. Se cita por primera vez para el área de estudio *Mengoana brigantina* (da Silva Mengo, 1867).

ABSTRACT

A faunistic study of species of superfamily Helicoidea Rafinesque, 1815, in the west of Galicia (La Coruña and Pontevedra provinces) has been realized. For each species the previous records and the coordinates U.T.M. 10x10 km of the localities where the species have been found, are included. Taking our own findings into consideration, and the data from bibliography, a map showing the distribution of each species has been drawn up, using U.T.M. 10x10 km system. *Mengoana brigantina* (da Silva Mengo, 1867) is recorded for the first time in this area.

PALABRAS CLAVE: Gastropoda, Pulmonata, Helicoidea, distribución, Galicia.
KEY WORDS: Gastropoda, Pulmonata, Helicoidea, distribution, Galicia.

INTRODUCCIÓN

El conocimiento de la fauna de moluscos terrestres de la Península Ibérica presentaba, hasta no hace mucho tiempo, un gran retraso respecto a Europa. Fue a finales del siglo XIX y principios del XX cuando se desarrolló más intensamente la actividad en este campo, y cuando comienza a otorgársele validez taxonómica a ciertas estructuras anatómicas, especialmente el

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aparato genital, tras comprobar que especies con conchas muy parecidas albergaban animales de organización anatómica diferente.

También en Galicia se inician, en este período, los estudios malacológicos con las aportaciones de autores como GRAELLS (1846), SEOANE (1866), MACHO VELADO (1871, 1878) e HIDALGO (1875). Posteriormente otros autores han realizado estudios en zonas geográficas concretas como ALTIMIRA (1969); SACCHI y VIOLANI (1977) y ROLÁN y OTERO (1988). Con mención específica a los helícidos cabe destacar el trabajo de CASTILLEJO (1981; 1986), que cubre gran parte del territorio gallego, recogiendo muestras en un total de 87 cuadrículas de 10x10 km U.T.M.

A pesar de estos estudios existen discontinuidades en la distribución de gran parte de las especies, motivo por el cual con el presente estudio queremos contribuir a ampliar el conocimiento faunístico de los gasterópodos terrestres pertenecientes a la superfamilia Helicoidea Rafinesque, 1815, aportando nuevos datos de distribución para las provincias de A Coruña y Pontevedra.

MATERIAL Y METODOS

Durante el período 1986-1989 se ha recolectado material malacológico procedente de las 176 cuadrículas U.T.M. de 10x10 km, en las que se han dividido las provincias de A Coruña y Pontevedra (Fig. 1a). En las distintas cuadrículas visitadas se han examinado detenidamente, de día y de noche, los distintos hábitats donde suelen resguardarse, recogiéndose además, muestras de suelo y hojarasca de distintos biotopos, que posteriormente se lavaron y tamizaron para separar los ejemplares.

Todos los gasterópodos capturados se sometieron al proceso habitual de muerte por anoxia sumergiéndolos en agua, para facilitar de este modo su disección, conservándose posteriormente en alcohol de 70°.

A partir de los datos obtenidos, se han elaborado los mapas de distribución de cada especie (Figs. 1b-g, Figs. 2a-l) en cuadrículas U.T.M. de 10x10 km, indicándose tanto las localidades aportadas en este trabajo (•) como las procedentes de la bibliografía (*), así como las localidades en las que se encontraron únicamente conchas vacías (O).

La colección malacológica se encuentra depositada en el Departamento de Biología Animal (Facultad de Biología, Universidad de Santiago de Compostela).

RESULTADOS

Se han identificado un total de 6873 ejemplares pertenecientes a 18 especies. Para cada especie se incluyen los siguientes apartados: citas previas, material estudiado (en el que se indica el número de ejemplares capturados en cada cuadrícula y aquellas localidades donde se encontraron conchas vacías), un breve resumen de su distribución geográfica y algunas observaciones de interés para aquellas especies en que lo hemos considerado necesario. El listado de las localidades junto a su correspondiente código, coordenadas U.T.M., Ayuntamiento y fecha de muestreo se pueden observar en la Tabla I.

Superfamilia HELICOIDEA Rafinesque, 1815
Familia XANTHONYCHIDAE Strebel y Pfeffer, 1880
Elona quimperiana (Férussac, 1821) (Fig. 1B)

Citas previas: CAZIOT (1915) como *H. quimperiana*; CASTILLEJO (1986); OTERO y TRIGO (1989).
Material examinado (107 ejemplares). **39**: 1; **58**: 1; **93**: 9; **94**: 3; **100**: 7; **102**: 1; **103**: 8; **104**: 12; **125**: 9; **130**: 1; **141**: 3; **143**: 2; **144**: 1; **145**: 5; **146**: 15; **147**: 14; **148**: 4; **156**: 6; **157**: 5.

Tabla I. Listado de las localidades, provincia, U.T.M. en 10 x 10 Km y fecha de recogida de las muestras, junto a su correspondiente código. C: A Coruña; L: Lugo; O: Ourense; P: Pontevedra.
Table I. List of the locations, provinces, U.T.M. 10x10 Km and sampling date, with its code. C: A Coruña; L: Lugo; O: Ourense; P: Pontevedra.

Código	Localidad/Ayuntamiento	Provincia	Coord. UTM	Fecha
1	*Caldelas de Tui*, Tui	P	29TNG35	26-09-86
2	*Cristelos*, Tomiño	P	29TNG15	26-09-86
3	*Louredo*, Mos	P	29TNG37	27-09-86
4	*Coruxo*, Vigo	P	29TNG17	27-09-86
5	*Pintos*, Pontevedra	P	29TNG39	28-09-86
6	*Dorrón*, Sanxenxo	P	29TNG19	28-09-86
7	*A Xesta*, A Lama	P	29TNG59	29-09-86
8	*O Covelo*, O Covelo	P	29TNG57	29-09-86
9	*Caldas de Reis*, Caldas de Reis	P	29TNH21	30-09-86
10	*Sobrido*, Ribeira	C	29TNH01	01-10-86
11	*Noal*, Porto do Son	C	29TNH03	01-10-86
12	*Sionlla*, Santiago	C	29TNH45	02-10-86
13	*Negreira*, Negreira	C	29TNH25	02-10-86
14	*Ponte Sarandón*, Vedra	P	29TNH43	03-10-86
15	*Arca*, A Estrada	P	29TNH41	03-10-86
16	*Ferreiros*, Vila de Cruces	P	29TNH64	04-10-86
17	*Prado*, Lalín	P	29TNH62	04-10-86
18	*Santa María*, Rodeiro	P	29TNH82	05-10-86
19	*Amance*, Golada	P	29TNH84	05-10-86
20	*Herbón*, Padrón	C	29TNH23	06-10-86
21	*Budiño*, Porriño	P	29TNG36	04-12-86
22	*Piñeiro*, O Covelo	P	29TNG58	04-12-86
23	*Salvaterra*, Salvaterra do Miño	P	29TNG45	05-12-86
24	*Arbo*, Arbo	P	29TNG56	05-12-86
25	*Loureza*, Oia	P	29TNG14	06-12-86
26	*Baredo*, Baiona	P	29TNG16	06-12-86
27	*Amoedo*, Pazos de Borbén	P	29TNG38	07-12-86
28	*Magdalena*, Cangas	P	29TNG18	07-12-86
29	*Leiro*, Ribadumia	P	29TNH20	08-12-86
30	*San Vicente do Grove*, O Grove	P	29TNH00	08-12-86
31	*Serrapio*, Cerdedo	P	29TNH40	09-12-86
32	*Nigoi*, A Estrada	P	29TNH42	09-12-86
33	*Vilatuxe*, Lalín	P	29TNH61	10-12-86
34	*Lagoa*, Dozón	P	29TNH81	10-12-86
35	*Barrio*, Vila de Cruces	P	29TNH63	11-12-86
36	*Ventosa*, Golada	P	29TNH83	11-12-86
37	*Catoira*, Catoira	P	29TNH22	12-12-86
38	*Boiro*, Boiro	C	29TNH02	12-12-86
39	*Lapido*, Ames	C	29TNH24	13-12-86
40	*Sergude*, Boqueixón	C	29TNH44	13-12-86
41	*Costa de Mougás*, Oia	P	29TNG05	10-04-87
42	*Camposancos*, A Guarda	P	29TNG13	11-04-87

Tabla I. Continuación.
Table I. Continuation.

Código	Localidad/Ayuntamiento	Provincia	Coord. UTM	Fecha
44	*Mondariz*, Mondariz	P	29TNG47	12-04-87
45	*Lavadores*, Vigo	P	29TNG27	12-04-87
46	*Pontecaldelas*, Pontecaldelas	P	29TNG49	13-04-87
47	*Postemirón*, Vilaboa	P	29TNG29	13-04-87
48	*Triñáns*, Boiro	C	29TNH11	14-04-87
49	*Oleiros*, Ribeira	C	29TMH91	15-04-87
50	*Portobravo*, Lousame	C	29TNH13	15-04-87
51	*César*, Caldas de Reis	P	29TNH31	16-04-87
52	*Carcacía*, Padrón	C	29TNH33	16-04-87
53	*Carballeda*, Lalín	P	29TNH72	17-04-87
54	*Baíña*, A Golada	P	29TNH74	17-04-87
55	*Quintás*, Touro	C	29TNH54	18-04-87
56	*Rellas*, Silleda	C	29TNH52	18-04-87
57	*Louro*, Muros	C	29TMH93	19-04-87
58	*Ordoeste*, A Baña	C	29TNH15	20-04-87
59	*A Peregrina*, Santiago	C	29TNH35	20-04-87
60	*Illas Cíes*, Vigo	P	29TNG07	12-05-87
61	*Barrantes*, Ribadumia	P	29TNH10	27-06-87
62	*Fontáns*, Barro	P	29TNH30	27-06-87
63	*Forcarei*, Forcarei	P	29TNH51	28-06-87
64	*Lamela*, Silleda	P	29TNH53	28-06-87
65	*Muimenta*, Lalín	P	29TNH73	29-06-87
66	*A Xesta*, Lalín	P	29TNH71	29-06-87
67	*Baroña*, Porto do Son	C	29TMH92	01-07-87
68	*Pontenafonso*, Noia	C	29TNH14	01-07-87
69	*Carreira*, Ribeira	C	29TMH90	02-07-87
70	*Bures*, Catoira	C	29TNH12	03-07-87
71	*Santa Mariña de Barcala*, A Estrada	P	29TNH32	03-07-87
72	*Oitavén*, Fornelos de Montes	P	29TNG48	04-07-87
73	*Ponteareas*, Ponteareas	P	29TNG46	04-07-87
74	*Moaña*, Moaña	P	29TNG28	05-07-87
75	*Mosende*, Porriño	P	29TNG26	06-07-87
76	*Tomiño*, Tomiño	P	29TNG24	06-07-87
77	*Chavella*, Oia	P	29TNG04	07-07-87
78	*Cabo Silleiro*, Baiona	P	29TNG06	07-07-87
79	*Santiago*, Santiago	C	29TNH34	08-07-87
80	*Esmorode*, Santa Comba	C	29TNH16	09-10-87
81	*Serra de Outes*, Serra de Outes	C	29TNH04	09-10-87
82	*Quilmas*, Carnota	C	29TMH84	10-10-87
83	*Vilela*, Muxía	C	29TMH76	10-10-87
84	*Berdoias*, Vimianzo	C	29TMH96	11-10-87
85	*Nande*, Laxe	C	29TMH98	11-10-87
86	*As Tarandeiras*, Coristanco	C	29TNH18	12-10-87

Tabla I. Continuación.
Table I. Continuation.

Código	Localidad/Ayuntamiento	Provincia	Coord. UTM	Fecha
88	*Rial*, Trazo	C	29TNH36	13-10-87
89	*Zas de Reis*, Melide	C	29TNH75	19-10-87
90	*Padreiro*, Curtis	C	29TNH77	19-10-87
91	*Xestal*, Irixoa	C	29TNH79	20-10-87
92	*Saa*, As Pontes	C	29TNJ91	20-10-87
93	*Freires*, Ortigueira	C	29TNJ93	21-10-87
94	*Regoa*, Cedeira	C	29TNJ73	21-10-87
95	*Esmelle*, Ferrol	C	29TNJ51	22-10-87
96	*Bouzarredonda*, Neda	C	29TNJ71	22-10-87
97	*Sigrás*, Cambre	C	29TNH59	23-10-87
98	*Abellá*, Frades	C	29TNH57	23-10-87
99	*Pedrouzo*, O Pino	C	29TNH55	24-10-87
100	*Viñas*, Paderne	C	29TNH69	18-01-88
101	*Neda*, Neda	C	29TNJ61	18-01-88
102	*Ponte de Mera*, Ortigueira	C	29TNJ83	19-01-88
103	*Mañón*, Mañón	C	29TPJ03	19-01-88
104	*Recemel*, Somozas	C	29TNJ81	20-01-88
105	*Boliqueiras*, As Pontes	C	29TNJ90	20-01-88
106	*Salto do Conexo*, Monfero	C	29TNH89	21-01-88
107	*Monte do Arco*, Curtis	C	29TNH87	22-01-88
108	*Rexidoira*, Cesuras	C	29TNH67	22-01-88
109	*Arzúa*, Arzúa	C	29TNH65	23-01-88
110	*Furelos*, Melide	C	29TNH85	23-01-88
111	*Vila da Igrexa*, Cerceda	C	29TNH48	24-01-88
112	*Parada*, Ordes	C	29TNH46	24-01-88
113	*Pedrafigueira*, Carnota	C	29TMH94	26-01-88
114	*Cabo Fisterra*, Fisterra	C	29TMH74	26-01-88
115	*Ozón*, Muxía	C	29TMH86	27-01-88
116	*Areosa*, Vimianzo	C	29TNH06	27-01-88
117	*Ponteceso*, Ponteceso	C	29TNH08	28-01-88
118	*Cances*, Carballo	C	29TNH28	28-01-88
119	*Bembibre*, Val do Dubra	C	29TNH26	29-01-88
120	*Sobrado dos Monxes*, Sobrado	C	29TNH76	25-03-88
121	*A Castellana*, Aranga	C	29TNH78	25-03-88
122	*A Capela*, A Capela	C	29TNJ70	26-03-88
123	*San Sadurniño*, San Sadurniño	C	29TNJ72	26-03-88
124	*O Ermo*, Ortigueira	C	29TNJ92	27-03-88
125	*Sismundi*, Ortigueira	C	29TNJ94	28-03-88
126	*Raxón*, Ferrol	C	29TNJ52	29-03-88
127	*Mabegondo*, Abegondo	C	29TNH58	30-03-88
128	*Carnoedo*, Sada	C	29TNJ50	30-03-88
129	*Poulo*, Ordes	C	29TNH56	31-03-88
130	*Río*, Cerceda	C	29TNH37	01-04-88

Tabla I. Continuación.
Table I. Continuation.

Código	Localidad/Ayuntamiento	Provincia	Coord. UTM	Fecha
132	*Agualada*, Coristanco	C	29TNH17	02-04-88
133	*Buño*, Malpica	C	29TNH19	02-04-88
134	*Santa Mariña*, Camariñas	C	29TMH88	03-04-88
135	*Ponte do Porto*, Camariñas	C	29TMH97	03-04-88
136	*Fisterra*, Fisterra	C	29TMH75	04-04-88
137	*Logoso*, Dumbría	C	29TMH95	05-04-88
138	*Arceo*, Boimorto	C	29TNH66	30-06-88
139	*Lagoa de Sobrado*, Sobrado	C	29TNH86	30-06-88
140	*Aranga*, Aranga	C	29TNH88	01-07-88
141	*Burricios*, Oza dos Ríos	C	29TNH68	01-07-88
142	*Faeira*, As Pontes	C	29TNJ80	02-07-88
143	*As Somozas*, Somozas	C	29TNJ82	02-07-88
144	*Grañas*, Mañón	C	29TPJ02	03-07-88
145	*Loiba*, Ortigueira	C	29TPJ04	03-07-88
146	*Serra da Capelada*, Ortigueira	C	29TNJ84	04-07-88
147	*Sedes*, Narón	C	29TNJ62	05-07-88
148	*Laraxe*, Cabanas	C	29TNJ60	05-07-88
149	*Ledoño*, Culleredo	C	29TNH49	06-07-88
150	*Leira*, Ordes	C	29TNH47	06-07-88
151	*Razo*, Carballo	C	29TNH29	07-07-88
152	*Canosa*, Carballo	C	29TNH27	07-07-88
153	*Corme*, Ponteceso	C	29TNH09	08-07-88
154	*Baio*, Zas	C	29TNH07	08-07-88
155	*Moraime*, Muxía	C	29TMH87	09-07-88
156	*Lobelos*, Cée	C	29TMH85	09-07-88
157	*A Picota*, Mazaricos	C	29TNH05	10-07-88
158	*Setados*, As Neves	P	29TNG55	17-03-89
159	*Crecente*, Crecente	P	29TNG66	17-03-89
160	*Paredes*, A Cañiza	P	29TNG67	18-03-89
161	*Pardesoa*, Forcarei	P	29TNH50	19-03-89
162	*Lira*, Carnota	C	29TMH83	22-04-89
163	*Couto*, Rodeiro	P	29TNH93	23-05-89
164	*Vilafrío*, Rodeiro	P	29TNH92	23-05-89
165	*San Pedro de Visma*, A Coruña	C	29TNJ40	30-05-89
166	*Sucadío*, As Pontes	C	29TPJ01	08-06-89
167	*Punta Candelaria*, Cedeira	C	29TNJ74	28-03-88
168	*Illa de Ons*, Bueu	P	29TNG09	31-05-89
169	*Momán*, Xermade	L	29TNH99	08-06-89
170	*Vilaverde*, Ribadavia	O	29TNG68	18-03-89
171	*Codesas*, Forcarei	P	29TNH60	19-03-89
172	*Cabo da Voutra*, Muxía	C	29TMH77	22-04-89
173	*Laxe*, Chantada	L	29TNH91	23-05-89
174	*Punta Frouxeira*, Valdoviño	C	29TNJ63	10-05-89
175	*Illa de Ons* (Sur), Bueu	P	29TNG09	31-05-89

Distribución geográfica: Se trata de una especie de distribución atlántico-europea (KERNEY, CAMERON Y JUNGBLUTH, 1983). Fuera de la Península Ibérica su área de distribución se restringe a la Bretaña francesa y al País Vasco francés (GERMAIN, 1930).

En la Península se limita a la costa septentrional. Está citada en el norte desde Galicia hasta el País Vasco (HIDALGO, 1875; GITTENBERGER, 1979; LARRAZ y JORDANA, 1984; CASTILLEJO, 1986; HERMIDA, OUTEIRO Y RODRÍGUEZ, 1992; PUENTE y PRIETO, 1992; LARRAZ y EQUISOAIN, 1993).

Familia HYGROMIIDAE Tryon, 1866

Candidula intersecta (Poiret, 1801) (Fig. 1C)

Citas previas: MACHO VELADO (1871) como *H. caperata*; HIDALGO (1875, 1890) como *H. caperata*; SACCHI y VIOLANI (1977) como *Helicella caperata*; CASTILLEJO (1986).
Material examinado (93 ejemplares). **6**: 1; **11**: 3; **19**: 1; **20**: 1; **30**: 1; **35**: 10; **37**: 1; **38**: 1; **42**: 3; **46**: 5; **47**: 2; **48**: 4; **49**: 6; **57**: 1; **60**: 6; **69**: 3; **74**: 3; **77**: 2; **78**: 5; **79**: 4; **82**: 1; **83**: 8; **93**: 6; **113**: 3; **114**: 4; **136**: 2; **137**: 1; **151**: 3; **156**: 2; **171**: 1.
Localidades con conchas vacías: **153**.

Distribución geográfica: Su área de distribución se enmarca en el oeste de Europa (KERNEY *ET AL.*, 1983).

En la Península se extiende por dos áreas, una en el sector norte oriental, el País Vasco y Navarra, y la otra en el tercio oeste, desde Galicia y centro de León hasta el Algarve, con algunas citas hacia el centro peninsular como Segovia (HIDALGO, 1875; NOBRE, 1941; RAMOS y APARICIO, 1985a; CASTILLEJO, 1986; HERMIDA *ET AL.*, 1992). En Asturias, desde la cita de ALTIMIRA (1969), no ha vuelto a ser encontrada (OJEA y ANADÓN, 1983; HERMIDA *ET AL.*, 1992), y tampoco se tiene constancia de ella en Cantabria.

Cernuella (Cernuella) virgata (da Costa, 1778) (Fig. 1D)

Citas previas: SACCHI y VIOLANI (1977); CASTILLEJO (1986).
Material examinado (3 ejemplares). **6**: 3.

Distribución geográfica: Especie mediterránea, ampliamente distribuida por el sur y oeste de Europa (KERNEY *ET AL.*, 1983).

Siendo común en el área peninsular y en las islas Baleares, es menos frecuente en la franja norte que comprende desde el valle del Tajo hasta el País Vasco, donde se convierte en una especie litoral (NOBRE, 1941; ORTIZ DE ZÁRATE y ORTIZ DE ZÁRATE, 1949; SEIXAS, 1976; PAUL, 1982; MANGA, 1983; LARRAZ y JORDANA, 1984; RAMOS y APARICIO, 1985b; CASTILLEJO, 1986; APARICIO, 1986; ROBLES, 1990; PUENTE y PRIETO, 1991, 1992; HERMIDA *ET AL.*, 1992; LARRAZ y EQUISOAIN, 1993; ALTONAGA, GÓMEZ, MARTÍN, PRIETO, PUENTE Y RALLO, 1994).

Helicella (Helicella) itala (Linneo, 1758) (Fig. 1E)

Citas previas: MACHO VELADO (1871) como *H. ericetorum*; HIDALGO (1875) como *H. ericetorum*; CASTILLEJO (1986); OTERO y TRIGO (1989).
Material examinado (32 ejemplares). **134**: 10; **151**: 20; **173**: 1; **174**: 1.

Distribución geográfica: Se trata de una especie distribuida por el oeste de Europa (KERNEY *ET AL.*, 1983).

En la Península Ibérica está presente en la mitad norte, siendo sus citas más escasas en Galicia (HIDALGO, 1875; HAAS,

1929; ORTIZ DE ZÁRATE y ORTIZ DE ZÁRATE, 1949; MANGA, 1983, APARICIO, 1986; CASTILLEJO, 1986; HERMIDA *ET AL.*, 1992; LARRAZ y EQUISOAIN, 1993; ALTONAGA *ET AL.*, 1994). En el área de estudio la hemos hallado únicamente en zonas del litoral.

Xerotricha apicina (Lamarck, 1822) (Fig. 1F)

Citas previas: MACHO VELADO (1871) como *H. apicina*; HIDALGO (1875, 1890) como *H. apicina*; ALTIMIRA (1969); SACCHI y VIOLANI (1977) como *Helicella apicina*; CASTILLEJO (1986).
Material examinado (3 ejemplares). **26**: 3.

Distribución geográfica: Es una especie con un área de distribución mediterránea (KERNEY *ET AL.*, 1983).

En la Península presenta una distribución costera bastante fragmentada, encontrándose en el norte unicamente en algunas localidades del litoral de Galicia (ALTIMIRA, 1969; SACCHI y VIOLANI, 1977; CASTILLEJO, 1986), Cantabria y Asturias (PUENTE y PRIETO, 1992). En el litoral mediterráneo está citada en Cataluña (HAAS, 1929; ALTIMIRA, 1969), Valencia (ROBLES, 1990); Málaga (ALTONAGA *ET AL.*, 1994), continuando desde ahí, de una forma más regular, por el cuadrante suroccidental hasta Aveiro en Portugal (SERVAIN, 1880; LOCARD, 1899; HIDALGO, 1875; NOBRE, 1941; RAMOS y APARICIO, 1985a) y hacia el interior hasta Badajoz. GASULL (1965) también la cita abundantemente en las Islas Baleares.

Cochlicella acuta (Müller, 1774) (Fig. 1G)

Citas previas: MACHO VELADO (1871) como *Bulimus acutus*; HIDALGO (1875) como *B. acutus*; HIDALGO (1890) como *H. acuta*; ALTIMIRA (1969); SACCHI y VIOLANI (1977); CASTILLEJO (1986); OTERO y TRIGO (1989).
Material examinado (99 ejemplares). **4**: 8; **6**: 8; **11**: 1; **26**: 9; **49**: 3; **57**: 4; **60**: 2; **69**: 4; **82**: 3; **83**: 8; **85**: 12; **93**: 5; **113**: 6; **136**: 10; **151**: 6; **156**: 4; **168**: 3; **173**: 3.

Distribución geográfica: Distribuida por la zona mediterránea y atlántica de Europa (BOATO, BODON Y GIUSTI, 1982).

Aparece practicamente en toda la costa ibérica e Islas Baleares (NOBRE, 1941; ORTIZ DE ZÁRATE y ORTIZ DE ZÁRATE, 1949; SACCHI, 1954; GASULL, 1965; ALTIMIRA, 1969; CASTILLEJO, 1986; BECH, 1990; MARTÍNEZ-ORTÍ, MARTÍNEZ-LÓPEZ, ROBLES Y RODRÍGUEZ BABÍO, 1990) penetrando en ocasiones hacia el interior siguiendo los valles fluviales. Está citada en puntos del interior como Salamanca (HERMIDA *ET AL.*, 1992), Huesca y Zaragoza (PUENTE y PRIETO, 1992).

Cochlicella barbara (Linneo, 1758) (Fig. 2A)

Citas previas: MACHO VELADO (1871) como *B. ventrosus*; HIDALGO (1875) como *B. ventrosus*; ALTIMIRA (1969) como *C. ventricosa*; SACCHI y VIOLANI (1977) como *C. ventricosa*; CASTILLEJO (1986) como *C. ventricosa*; OTERO y TRIGO (1989) como *C. ventricosa*.
Material examinado (704 ejemplares). **1**: 3; **2**: 1; **3**: 2; **4**: 6; **5**: 4; **6**: 17; **9**: 16; **11**: 12; **21**: 1; **24**: 3; **25**: 7; **26**: 218; **27**: 5; **29**: 2; **30**: 1; **37**: 1; **38**: 6; **43**: 2; **44**: 1; **47**: 8; **48**: 20; **49**: 82; **50**: 1; **51**: 1; **52**: 4; **57**: 8; **60**: 4; **61**: 5; **68**: 1; **69**: 73; **70**: 2; **73**: 15; **74**: 12; **76**: 16; **81**: 3; **82**: 3; **83**: 2; **85**: 8; **86**: 2; **93**: 6; **94**: 17; **95**: 1; **97**: 22; **113**: 19; **117**: 1; **118**: 2; **126**: 1; **128**: 1; **132**: 6; **133**: 7; **135**: 1; **136**: 6; **148**: 5; **149**: 7; **151**: 6; **156**: 4; **168**: 12; **174**: 2.
Localidades con conchas vacías: **127**.

Distribución geográfica: Especie con un amplio rango de distribución en el área mediterránea y a lo largo de las costas del oeste de Europa (BACKHUYS, 1975).

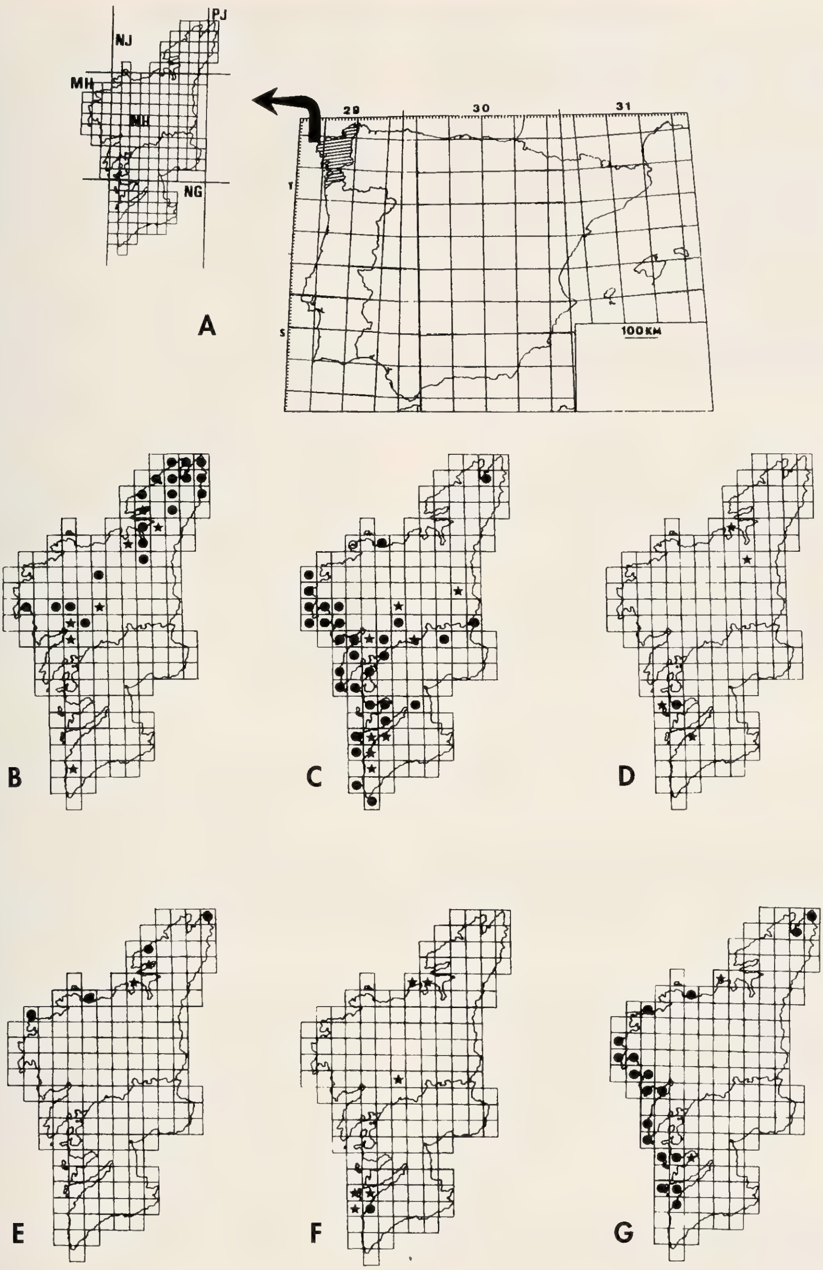

Figura 1. A: Area de estudio en la Península Ibérica. B-G: Mapas de distribución. B: *Elona quimperiana*; C: *Candidula intersecta*; D: *Cernuella virgata*; E: *Helicella itala*; F: *Xerotricha apicina*; G: *Cochlicella acuta*. Localidades citadas en este trabajo (•); procedentes de la bibliografía (*); únicamente encontradas conchas vacías (O).

Figure 1: A: The study area in the Iberian Peninsula. B-G: Distribution maps. B: Elona quimperiana*; C:* Candidula intersecta*; D:* Cernuella virgata*; E:* Helicella itala*; F:* Xerotricha apicina*; G:* Cochlicella acuta. *Localities reported in this paper (•); bibliographic records (*); only shells found (O).*

En la Península presenta una distribución bastante amplia, y aunque aparece con mayor frecuencia en el litoral, citándose en casi todas las provincias estudiadas (BOFILL y HAAS, 1920a; NOBRE, 1941; ALTIMIRA, 1969; OJEA y ANADÓN, 1983; RAMOS y APARICIO, 1985b, CASTILLEJO, 1986; MARTÍNEZ-ORTÍ *ET AL.*, 1990; PUENTE y PRIETO, 1991, 1992; HERMIDA *ET AL.*, 1992; LARRAZ y EQUISOAIN, 1993; PAREJO *ET AL.*, 1993b). También se ha encontrado en las islas Baleares (GASULL, 1965; PAUL, 1982). En la zona de estudio está ligada a la franja litoral, aunque penetra más hacia el interior que *C. acuta* y *C. conoidea.*

Cochlicella conoidea (Draparnaud, 1801) (Fig. 2B)

Citas previas: MACHO VELADO (1871) como *B. pringi;* HIDALGO (1875) como *B. pringi;* HIDALGO (1890) como *H. conoidea;* SACCHI y VIOLANI (1977); OTERO y TRIGO (1989).
Material examinado (79 ejemplares). **4**: 9; **6**: 8; **49**: 3; **57**: 4; **60**: 1; **82**: 4; **83**: 20; **113**: 4; **136**: 20; **156**: 6.

Distribución geográfica: Especie común a lo largo de la costa mediterránea, desde los Pirineos orientales hasta los Alpes marítimos (KERNEY *ET AL.*, 1983)

En la Península se encuentra en el litoral mediterráneo, aunque también está citada en la costa atlántica portuguesa y gallega, y aisladamente y con escasos ejemplares en el interior (LOCARD, 1899; HAAS, 1929; NOBRE, 1941; SACCHI, 1954; GASULL, 1965; ALTIMIRA, 1969; GASULL, 1975; SACCHI y VIOLANI, 1977; RAMOS y APARICIO, 1985b; CASTILLEJO, 1986; MARTÍNEZ-ORTÍ *ET AL.*, 1990). La única cita existente en el litoral cantábrico dada por ORTIZ DE ZÁRATE y ORTIZ DE ZÁRATE (1949) ha sido asignada por distintos autores a *C. barbara* (PUENTE y PRIETO, 1992).

Ashfordia granulata (Alder, 1830) (Fig. 2C)

Citas previas: MACHO VELADO (1871) como *H. sericea;* HIDALGO (1875) como *H. sericea;* CASTILLEJO (1986) como *Monacha (Ashfordia) granulata.*
Material examinado (151 ejemplares). **6**: 1; **35**: 6; **53**: 1; **69**: 3; **79**: 24; **83**: 1; **90**: 5; **93**: 5; **94**: 23; **95**: 13; **96**: 1; **97**: 14; **102**: 11; **115**: 2; **117**: 3; **118**: 1; **120**: 3; **135**: 22; **143**: 1; **145**: 1; **149**: 2; **153**: 2; **155**: 3; **165**: 3.

Distribución geográfica: Se distribuye por el oeste de Europa (KERNEY *ET AL.*, 1983).

En la Península Ibérica su área de distribución comprende desde Galicia hasta el extremo occidental de Vizcaya, penetrando hacia León (MANGA, 1983; ANADÓN y OJEA, 1984; HOLYOAK y SEDDON, 1985; CASTILLEJO, 1986; HERMIDA *ET AL.*, 1992; PUENTE y PRIETO, 1992).

Zenobiella subrufescens (Miller, 1822) (Fig. 2D)

Citas previas: CASTILLEJO (1986) como *Monacha (Zenobiella) subrufescens.*
Material examinado (34 ejemplares). **39**: 1; **40**: 1; **50**: 4; **68**: 1; **79**: 1; **87**: 5; **90**: 2; **93**: 3; **94**: 2; **97**: 1; **102**: 2; **108**: 1; **111**: 1; **116**: 1; **117**: 5; **118**: 1; **128**: 1; **162**: 1.
Localidades con conchas vacías: **13**, **58**.

Distribución geográfica: Se extiende por el oeste europeo (KERNEY *ET AL.*, 1983). Según GERMAIN (1930) no se aleja de las regiones de influencia marítima.

En la Península Ibérica está citada unicamente en la franja norte que comprende desde Galicia hasta el País Vasco y Navarra (OJEA y ANADÓN, 1983; CASTILLEJO, 1986, HERMIDA *ET AL.*, 1992; PUENTE y PRIETO, 1992; LARRAZ y EQUISOAIN, 1993; ALTONAGA *ET AL.*, 1994).

Portugala inchoata (Morelet, 1845) (Fig. 2E)

Citas previas: MACHO VELADO (1871) como *H. inchoata;* HIDALGO (1875, 1890) como *H. inchoata;* GITTENBERGER (1980); SACCHI (1981) como *Monachoides inchoatus;* CASTILLEJO (1986); OTERO y TRIGO (1989).
Material examinado (928 ejemplares). **1**: 11; **2**: 17; **3**: 7; **4**: 7; **5**: 7; **6**: 20; **8**: 5; **9**: 11; **10**: 2; **11**: 7; **12**: 8; **13**: 1; **14**: 2; **16**: 16; **17**: 3; **18**: 2; **19**: 5; **20**: 4; **21**: 19; **22**: 4; **23**: 1; **24**: 13; **25**: 13; **26**: 6; **27**: 4; **28**: 11; **29**: 10; **30**: 3; **31**: 4; **32**: 3; **33**: 1; **35**: 10; **36**: 3; **37**: 1; **38**: 8; **39**: 16; **40**: 4; **41**: 14; **42**: 12; **43**: 5; **44**: 4; **45**: 7; **46**: 7; **47**: 9; **48**: 17; **49**: 3; **50**: 12; **51**: 1; **52**: 8; **53**: 2; **54**: 6; **55**: 5; **56**: 4; **57**: 3; **58**: 2; **59**: 2; **60**: 21; **61**: 10; **62**: 4; **63**: 1; **64**: 6; **65**: 5; **67**: 8; **68**: 4; **69**: 6; **70**: 9; **71**: 2; **72**: 5; **73**: 3; **74**: 24; **75**: 17; **76**: 15; **77**: 7; **78**: 5; **79**: 9; **80**: 10; **81**: 2; **82**: 3; **83**: 10; **84**: 2; **85**: 5; **86**: 14; **87**: 1; **88**: 1; **89**: 3; **90**: 1; **91**: 2; **93**: 4; **94**: 5; **95**: 8; **96**: 2; **97**: 9; **98**: 1; **99**: 6; **100**: 5; **101**: 7; **103**: 1; **104**: 2; **105**: 1; **106**: 5; **107**: 3; **108**: 1; **109**: 3; **110**: 4; **111**: 11; **112**: 15; **113**: 3; **114**: 3; **115**: 5; **116**: 4; **117**: 12; **118**: 7; **119**: 3; **121**: 6; **123**: 1; **124**: 1; **125**: 13; **127**: 1; **128**: 4; **129**: 1; **130**: 2; **131**: 4; **132**: 2; **133**: 4; **135**: 4; **136**: 21; **137**: 8; **138**: 2; **139**: 2; **140**: 1; **141**: 2; **142**: 4; **143**: 7; **145**: 6; **146**: 5; **147**: 2; **148**: 3; **149**: 4; **150**: 2; **151**: 8; **152**: 5; **153**: 13; **154**: 1; **155**: 8; **156**: 8; **157**: 4; **158**: 5; **160**: 1; **161**: 2; **162**: 4; **164**: 2; **165**: 2; **167**: 2; **168**: 3; **170**: 1; **171**: 8; **172**: 2.
Localidades con conchas vacías: **15**.

Distribución geográfica: Esta especie es endémica del oeste de la Península Ibérica (NOBRE, 1941; GITTENBERGER, 1980).

Está citada en el norte, centro y sur de Portugal por diversos autores (MORELET, 1877; SERVAIN, 1880; LOCARD, 1899; NOBRE, 1941; RAMOS y APARICIO, 1985a) y en toda la franja oeste española desde Asturias a Huelva (MANGA, 1983; HERMIDA *ET AL.*, 1992; PUENTE y PRIETO, 1992). En Galicia es uno de los elementos más característicos de su malacofauna.

Ponentina subvirescens (Bellamy, 1839) (Fig. 2F)

Citas previas: MACHO VELADO (1871) como *H. occidentalis;* HIDALGO (1875) como *H. occidentalis;* SACCHI y VIOLANI (1977) como *Trichia occidentalis;* CASTILLEJO (1986) como *Ponentina ponentina.*
Material examinado (321 ejemplares). **1**: 2; **2**: 2; **4**: 1; **19**: 3; **21**: 5; **26**: 6; **30**: 1; **32**: 1; **36**: 3; **38**: 1; **41**: 4; **42**: 14; **43**: 10; **44**: 3; **45**: 2; **47**: 7; **48**: 3; **49**: 4; **50**: 10; **51**: 1; **52**: 8; **54**: 2; **57**: 5; **59**: 1; **60**: 6; **61**: 1; **70**: 1; **76**: 2; **77**: 2; **79**: 1; **86**: 1; **89**: 1; 91: 2; **97**: 2; **99**: 5; **103**: 3; **107**: 2; **109**: 1; **110**: 1; **111**: 3; **112**: 1; **113**: 1; **114**: 9; **115**: 2; **117**: 1; **119**: 119; **122**: 7; **132**: 3; **133**: 2; **134**: 22; **135**: 1; **137**: 2; **138**: 1; **146**: 7; **153**: 8; **169**: 2.
Localidades con conchas vacías: **3**; **6**; **9**; **22**; **23**; **24**; **25**; **28**; **29**; **34**; **39**; **53**; **73**; **83**; **88**; **120**; **121**; **127**; **131**; **142**; **148**; **151**; **159**; **160**.

Distribución geográfica: Especie atlántica que se distribuye por el suroeste de Europa (KERNEY *ET AL.*, 1983), perteneciente a la fauna atlantico-lusitánica.

En la Península se distribuye a lo largo de todo su tercio oeste (LOCARD, 1899; NOBRE, 1941; MANGA, 1983; CASTILLEJO, 1986; HERMIDA *ET AL.*, 1992; PUENTE y PRIETO, 1992). Los puntos más orientales corresponden a La Rioja, Burgos y Alava (PUENTE y PRIETO, 1992).

Mengoana brigantina (da Silva Mengo, 1867) (Fig. 2G)

Material examinado (3 ejemplares). **9**: 1; **67**: 1; **128**: 1.

Distribución geográfica: Esta especie es un endemismo ibérico restringido al noroeste de la Península.

Su área de distribución se extiende desde el extremo nororiental de Portugal, hasta el oeste de Vizcaya (HIDALGO, 1875; ORTIZ DE ZARATE, 1949; RAMOS y APARICIO, 1985a; MANGA, 1983; HERMIDA *ET AL.*, 1992; PUENTE y PRIETO, 1992). Hasta este momento su límite occidental se encontraba en el este de Galicia (CASTILLEJO, 1986).

Observaciones: Se trata de la cita más occidental de las conocidas y de la primera para el área de estudio, encontrándose en zonas costeras. Su carácter calcícola puede ser la causa de que hayamos recogido un escaso número de ejemplares en nuestra área de estudio, predominantemente granítica.

Este taxon presenta una cierta controversia dado que el holotipo de esta especie, citada como *Helix brigantina* (da Silva Mengo, 1867) y recogido en Bragança (Portugal), se ha extraviado, conservándose únicamente su descripción, sin ningún dibujo o representanción y sin que haya vuelto a encontrarse ningún ejemplar en la localidad tipo. ROSSMASSLER (1879) figura un ejemplar de esta especie, aportando otros datos a su descripción y señalando una nueva localidad en el norte de la Península (La Liébana, Cantabria). NOBRE (1941) no encuentra esta especie en ningún punto de Portugal y presupone que la especie descrita por DA SILVA MENGO (1867) podría tratarse de una variedad *minor* de *Helix inchoata* (Morelet, 1879). Este problema persiste hoy en día y sigue siendo necesario comprobar si el genital de los individuos encontrados en los alrededores de Bragança coincide con el representado por ORTIZ DE ZÁRATE (1949). De no ser así, lo que ahora se conoce como *Mengoana brigantina* en el norte de la Península debería ser considerada como *Mengoana jeschaui* (ORTIZ DE ZÁRATE, 1949).

Oestophora (Oestophora) barbula (Rossmässler, 1838) (Fig. 2h)

Citas previas: GRAELLS (1846) como *H. holosericea*; MACHO VELADO (1871) como *H. barbula*; HIDALGO (1875, 1890) como *H. barbula*; ORTIZ DE ZÁRATE (1962); SACCHI y VIOLANI (1977); CASTILLEJO (1984); OTERO y TRIGO (1989).

Material examinado (661 ejemplares). **1**: 10; **2**: 4; **3**: 7; **4**: 8; **5**: 2; **6**: 3; **7**: 1; **9**: 2; **10**: 1; **11**: 1; **14**: 7; **17**: 2; **19**: 2; **20**: 4; **21**: 2; **22**: 2; **23**: 4; **24**: 5; **25**: 10; **26**: 14; **27**: 6; **28**: 9; **29**: 20; **30**: 7; **32**: 2; **35**: 10; **37**: 15; **39**: 15; **41**: 17; **42**: 26; **43**: 7; **45**: 2; **46**: 3; **47**: 1; **48**: 11; **49**: 3; **51**: 6; **52**: 5; **53**: 1; **54**: 1; **56**: 2; **57**: 6; **58**: 8; **59**: 3; **60**: 7; **61**: 1; **62**: 1; **67**: 2; **68**: 4; **69**: 33; **70**: 1; **74**: 2; **77**: 5; **79**: 4; **81**: 4; **82**: 2; **83**: 10; **84**: 3; **85**: 1; **86**: 14; **87**: 6; **88**: 2; **89**: 4; **94**: 2; **95**: 2; **96**: 1; **97**: 8; **98**: 2; **99**: 3; **101**: 4; **109**: 6; **110**: 7; **112**: 1; **113**: 23; **114**: 17; **115**: 4; **116**: 2; **117**: 8; **118**: 3; **119**: 5; **120**: 6; **122**: 1; **123**: 4; **127**: 8; **128**: 5; **129**: 5; **130**: 1; **132**: 2; **134**: 1; **135**: 34; **136**: 7; **137**: 4; **138**: 8; **139**: 1; **143**: 1; **145**: 2; **149**: 10; **150**: 1; **151**: 3; **152**: 8; **153**: 15; **154**: 2; **155**: 7; **156**: 8; **157**: 1; **158**: 8; **161**: 6; **168**: 7; **171**: 14.

Localidades con conchas vacías: **15**.

Distribución geográfica: Esta especie es un endemismo ibérico perteneciente a la fauna atlántico lusitánica.

Está presente en todo el oeste peninsular, desde Galicia y Asturias hasta el sur de Portugal y Huelva, adentrándose en algunos puntos del centro peninsular (NOBRE, 1941; ORTIZ DE ZÁRATE, 1962; ALTIMIRA, 1969; MANGA, 1983; RAMOS y APARICIO, 1985a; CASTILLEJO, 1984; HERMIDA *ET AL.*, 1992). Alejada de este área se ha citado también en sureste ibérico (HIDALGO, 1875; GASULL, 1975) y Pirineos.

Oestophora (Oestophora) silvae Ortiz de Zárate López, 1962 (Fig. 2I)

Citas previas: HIDALGO (1875, 1890) como *O. lusitanica*; ORTIZ DE ZÁRATE (1962); CASTILLEJO (1984) como *O. lusitanica* var. *minor*; OTERO y TRIGO (1989).

Material examinado (474 ejemplares). **1**: 16; **3**: 1; **4**: 2; **5**: 5; **7**: 3; **8**: 2; **13**: 1; **14**: 4; **18**: 2; **19**: 1; **21**: 8; **22**: 7; **23**: 3; **24**: 17; **25**: 27; **26**: 9; **27**: 14; **28**: 2; **31**: 2; **32**: 1; **33**: 13; **35**: 4; **37**: 29; **39**: 7; **40**: 34; **41**: 39; **42**: 8; **43**: 10; **44**: 7; **45**: 2; **46**: 9; **47**: 9; **50**: 13; **51**: 3; **53**: 15; **54**: 2; **55**: 2; **56**: 1; **58**: 5; **62**: 1; **63**: 3; **71**: 2; **75**: 1; **77**: 7; **82**: 1; **84**: 3; **88**: 1; **90**: 2; **91**: 2; **99**: 18; **100**: 10; **106**: 3; **108**: 7; **109**: 7; **110**: 10; **111**: 1; **115**: 9; **120**: 1; **121**: 16; **130**: 1; **137**: 4; **138**: 1; **141**: 6; **154**: 1; **155**: 1; **158**: 1; **159**: 6; **160**: 3; **166**: 2; **170**: 4.

Localidades con conchas vacías: **16**; **87**; **93**.

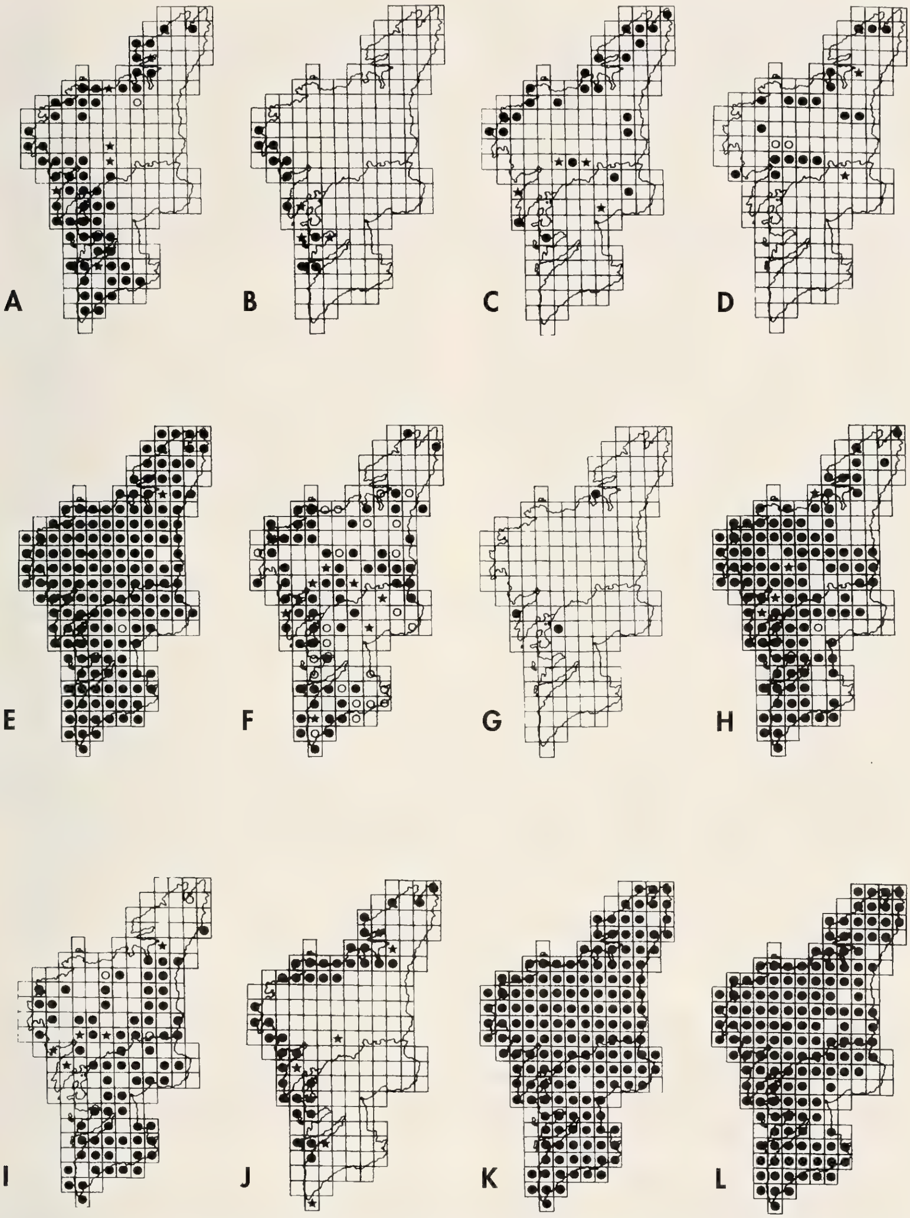

Figura 2. Mapas de distribución. A: *Cochicella barbara*; B: *Cochlicella conoidea*; C: *Ashfordia granulata*; D: *Zenobiella subrufescens*; E: *Portugala inchoata*; F: *Ponentina subvirescens*; G: *Mengoana brigantina*; H: *Oestophora barbula*; I: *Oestophora silvae*; J: *Theba pisana*; K: *Cepaea nemoralis*; L: *Helix aspersa*. Localidades citadas en este trabajo (•); procedentes de la bibliografía (*); únicamente encontradas conchas vacías (O).

Figure 2: Distribution maps. A: Cochlicella barbara*; B:* Cochlicella conoidea*; C:* Ashfordia granulata*; D:* Zenobiella subrufescens*; E:* Portugala inchoata*; F:* Ponentina subviresens*; G:* Mengoana brigantina*; H:* Oestophora barbula*; I:* Oestophora silvae*; J:* Theba pisana*; K:* Cepaea nemoralis*; L:* Helix aspersa. *Localities reported in this paper (•); bibliographic records (*); only shells found (O).*

Distribución geográfica: Es un endemismo ibérico restringido al norte de la Península, desde Galicia hasta el norte de Alava (Castillejo, 1986; Ojea y Anadón, 1983; Puente y Prieto, 1992; Hermida, *et al.*, 1992).

Observaciones: Ortiz de Zárate (1962) al describir *O. silvae* expuso las diferencias que existían entre esta especie y *Oestophora lusitanica* (Pfeiffer, 1841). Señala que *O. silvae* es más pequeña, tiene el borde superior de la abertura más corto, un engrosamiento mayor del peristoma en toda su extensión, presenta una callosidad blanca interna en el extremo del borde superior de la última vuelta con la antepenúltima y carece del estriado espiral en la cara inferior, cerca de la abertura, que caracteriza a *O. lusitanica*. Respecto al aparato genital destaca la distinta inserción del músculo retractor del pene, que se sitúa hacia la mitad de la vaina en *O. lusitanica* y cerca del extremo en *O. silvae*, y la distinta longitud de las glándulas multífidas y del oviducto libre, mucho más cortos en *O. silvae*.

Según Ortiz de Zárate (1962) *O. silvae* es la misma especie que fue descrita por da Silva en 1871 como *O. lusitanica* var. *minor*. Así mismo asigna a esta especie todas las citas de *O. lusitanica*, dadas por Hidalgo (1875), para el norte de la Península y Galicia. Sin embargo Castillejo (1984) encontró, en diversos puntos de Galicia, ejemplares que no coincidían completamente con la descripción de *O. silvae*, siendo más similar a la de *O. lusitanica* var. *minor*, a la que asignó esos ejemplares.

Nosotros hemos podido estudiar individuos de *O. lusitanica* de Portugal, y ninguno de nuestros ejemplares gallegos se ajusta a las características de esta especie. Respecto a *O. silvae*, hemos observado que los datos de la descripción de Ortiz de Zárate (1962) deberían ser revisados, ya que existen ejemplares de mayor diámetro que el señalado por él, y una observación detallada de la concha húmeda pone de manifiesto, en todos los ejemplares, las estrías espirales en la cara inferior que, en un principio, sólo parecía presentar *O. lusitanica*. En lo referente al aparato genital, las glándulas multífidas pueden ser más largas que las descritas y el músculo retractor del pene presenta cierta variabilidad en su inserción. Observadas estas variaciones y una vez estudiados los ejemplares de nuestra colección y la del Dr. Castillejo, hemos seguido a Ortiz de Zárate considerando las citas gallegas de *O. lusitanica* var. *minor* como *O. silvae*.

Familia Helicidae Rafinesque, 1815

Theba pisana (Müller, 1774) (Fig. 2J)

Citas previas: Macho Velado (1871) como *H. pisana*; Hidalgo (1875, 1890) como *H. pisana*; Sacchi y Violani (1977) como *Euparipha pisana*; Castillejo (1986); Otero y Trigo (1989).
Material examinado (373 ejemplares). **4**: 20; **6**: 3; **11**: 3; **26**: 10; **30**: 2; **48**: 1; **49**: 1; **57**: 14; **60**: 2; **67**: 5; **69**: 50; **82**: 1; **83**: 4; **85**: 12; **86**: 5; **87**: 10; **91**: 10; **93**: 2; **94**: 17; **95**: 1; **97**: 3; **100**: 3; **113**: 7; **117**: 1; **118**: 12; **126**: 9; **128**: 1; **131**: 33; **133**: 12; **136**: 15; **149**: 35; **151**: 25; **153**: 10; **156**: 3; **165**: 2; **168**: 5; **173**: 24.

Distribución geográfica: Esta especie presenta una distribución circunmediterránea que remonta las costas atlánticas hasta Inglaterra (Kerney *et al.*, 1983).

En la Península se extiende a lo largo de toda la costa, aunque es capaz de colonizar áreas del interior cuando se dan condiciones adecuadas, tales como disponibilidad de sales solubles (Prieto, *com. pers.*). Como citas más recientes en el interior se pueden señalar las dadas por Hermida *et al.* (1992) y Parejo *et al.* (1993b).

Cepaea (Cepaea) nemoralis (Linneo, 1758) (Fig. 2K)

Citas previas: Macho Velado (1871) como *H. nemoralis*; Hidalgo (1875, 1890) como *H. nemoralis*; Sacchi y Violani (1977); Sacchi (1981); Castillejo (1986); Otero y Trigo (1989).

Material examinado (1229 ejemplares). **1**: 32; **2**: 13; **3**: 10; **4**: 7; **5**: 3; **6**: 11; **7**: 2; **8**: 4; **9**: 4; **10**: 1; **11**: 4; **12**: 4; **13**: 4; **14**: 7; **16**: 8; **17**: 3; **18**: 4; **19**: 4; **20**: 2; **21**: 5; **22**: 9; **23**: 3; **24**: 9; **25**: 17; **26**: 8; **27**: 9; **28**: 10; **29**: 4; **30**: 15; **31**: 4; **32**: 10; **33**: 4; **35**: 1; **36**: 12; **37**: 4; **38**: 12; **39**: 12; **40**: 5; **41**: 28; **42**: 2; **43**: 8; **44**: 5; **45**: 12; **46**: 12; **47**: 15; **48**: 13; **49**: 7; **50**: 7; **51**: 9; **52**: 3; **53**: 1; **54**: 9; **55**: 5; **56**: 4; **57**: 7; **58**: 2; **59**: 6; **61**: 9; **62**: 2; **63**: 9; **64**: 11; **65**: 1; **66**: 1; **67**: 12; **68**: 2; **69**: 1; **70**: 5; **71**: 7; **72**: 10; **73**: 2; **74**: 4; **75**: 10; **76**: 6; **77**: 20; **79**: 6; **80**: 7; **81**: 8; **82**: 4; **83**: 12; **84**: 11; **85**: 3; **86**: 10; **87**: 11; **88**: 6; **89**: 7; **90**: 8; **91**: 2; **92**: 6; **93**: 17; **94**: 3; **95**: 11; **96**: 12; **97**: 10; **98**: 4; **99**: 14; **100**: 14; **101**: 8; **102**: 20; **103**: 2; **104**: 9; **105**: 2; **106**: 4; **107**: 2; **108**: 10; **109**: 15; **110**: 23; **111**: 8; **112**: 14; **113**: 16; **114**: 7; **115**: 12; **116**: 13; **117**: 26; **118**: 8; **119**: 8; **120**: 12; **121**: 11; **122**: 7; **123**: 11; **125**: 7; **126**: 1; **127**: 10; **128**: 5; **129**: 8; **130**: 3; **131**: 11; **132**: 12; **133**: 14; **134**: 3; **135**: 6; **136**: 4; **137**: 5; **138**: 7; **139**: 6; **140**: 1; **141**: 10; **142**: 8; **143**: 8; **144**: 4; **145**: 5; **146**: 20; **147**: 12; **148**: 7; **149**: 8; **150**: 5; **151**: 4; **152**: 7; **153**: 12; **154**: 2; **155**: 3; **156**: 7; **157**: 3; **158**: 1; **159**: 2; **160**: 1; **161**: 3; **162**: 2; **163**: 2; **164**: 1; **165**: 2; **166**: 1; **170**: 2; **171**: 3.

Distribución geográfica: Presenta una distribución centro-occidental europea (BOATO *ET AL.*, 1982).

En la Península Ibérica se extiende por la franja portuguesa (HIDALGO, 1875; LOCARD, 1899; NOBRE, 1941) y por toda la mitad norte (BOFILL y HAAS, 1919, 1920a, 1920b; ORTIZ DE ZÁRATE y ORTIZ DE ZÁRATE, 1949; MANGA, 1983; RAMOS, 1985; APARICIO, 1986; HERMIDA *ET AL.*, 1992; LARRAZ y EQUISOAIN, 1993; PAREJO *ET AL.*, 1993b; ALTONAGA *ET AL.*, 1994). En la mitad sur peninsular es más frecuente en Portugal, pero en los últimos años varios autores han ampliado su distribución en esta zona (MARTÍNEZ-ORTI y ROBLES, 1993; PAREJO, *ET AL.*, 1993a).

Helix (Cornu) aspersa (Müller, 1774) (Fig. 2L)

Citas previas: MACHO VELADO (1871); HIDALGO (1875, 1890); SACCHI y VIOLANI (1977) como *Cryptomphalus aspersus*; CASTILLEJO (1986); OTERO y TRIGO (1989).
Material examinado (1579 ejemplares). **1**: 1; **2**: 1; **3**: 5; **4**: 32; **5**: 3; **6**: 12; **8**: 4; **9**: 6; **10**: 1; **11**: 3; **12**: 5; **13**: 12; **14**: 3; **16**: 2; **17**: 3; **19**: 5; **20**: 7; **21**: 30; **22**: 4; **23**: 4; **24**: 3; **25**: 6; **26**: 16; **27**: 6; **28**: 54; **29**: 15; **30**: 9; **31**: 3; **32**: 12; **35**: 18; **36**: 8; **37**: 20; **38**: 17; **39**: 15; **40**: 13; **41**: 28; **42**: 22; **43**: 2; **44**: 12; **45**: 17; **46**: 11; **47**: 4; **48**: 26; **49**: 18; **50**: 11; **51**: 20; **52**: 22; **53**: 20; **54**: 11; **55**: 10; **56**: 7; **57**: 19; **58**: 1; **59**: 12; **60**: 11; **61**: 21; **62**: 9; **63**: 1; **64**: 27; **65**: 2; **67**: 23; **68**: 16; **69**: 12; **70**: 14; **71**: 11; **73**: 6; **75**: 13; **76**: 4; **77**: 7; **78**: 1; **79**: 6; **80**: 2; **81**: 10; **82**: 10; **83**: 5; **84**: 5; **85**: 8; **86**: 10; **87**: 10; **88**: 10; **90**: 2; **91**: 17; **92**: 11; **93**: 16; **94**: 16; **95**: 14; **96**: 11; **97**: 9; **98**: 9; **100**: 14; **101**: 42; **102**: 48; **103**: 21; **104**: 5; **106**: 10; **109**: 10; **110**: 7; **111**: 4; **112**: 6; **113**: 17; **114**: 22; **115**: 14; **116**: 2; **117**: 36; **118**: 8; **119**: 15; **120**: 16; **121**: 11; **122**: 11; **123**: 36; **124**: 3; **125**: 9; **126**: 8; **127**: 13; **128**: 9; **129**: 12; **130**: 2; **131**: 11; **132**: 16; **133**: 8; **134**: 22; **135**: 5; **136**: 10; **137**: 12; **138**: 2; **139**: 1; **141**: 3; **143**: 4; **144**: 1; **145**: 8; **146**: 16; **147**: 4; **148**: 6; **149**: 6; **150**: 1; **151**: 3; **152**: 2; **153**: 9; **154**: 2; **155**: 5; **156**: 2; **157**: 1; **158**: 2; **159**: 1; **160**: 4; **162**: 3; **165**: 3; **167**: 1; **168**: 1; **171**: 3.

Distribución geográfica: Especie distribuida por el Mediterráneo y oeste de Europa. (BOATO *ET AL.*, 1982).

En la Península Ibérica se ha citado repetidamente en todas las regiones (ALTONAGA *ET AL.*, 1994) y en las Islas Baleares, y aún faltando zonas por estudiar, dado su carácter ubiquista y sinantrópico, puede asegurarse que está presente en todo el territorio peninsular.

DISCUSIÓN

En un principio y dadas las condiciones climáticas gallegas favorables para la vida de los gasterópodos terrestres, podríamos pensar que es un área de abundante fauna malacológica. Pero comparándola con otras zonas de la Península Ibérica enclavadas en el área atlántica podemos comprobar que la diversidad y abundancia de helícidos es especialmente escasa en Galicia. Probablemente esto es debido, principalmente, a la escasez de sustrato calizo, necesario para la formación de la concha de todos los gasterópodos en general y, de la conchas gruesas y duras de los helícidos en particular (BOYCOTT, 1934; KERNEY y CAMERON, 1983).

Con este trabajo se ha ampliado el área de distribución conocida de la mayor parte de las especies, pudiendo señalar la notable presencia en la zona de estudio de especies como *H. aspersa, C. nemoralis* y *P. inchoata*, que aparecen en más del 80% de las cuadrículas visitadas. A diferencia de ésto, existen otras especies que han presentado distribuciones restringidas, especialmente aquellas originariamente mediterráneas, intimamente ligadas al litoral como *T. pisana, C. acuta, C. barbara,* y *C. conoidea*, destacando especialmente esta última, que al igual que sucede en el resto de la Península, no asciende por la costa cantábrica. En contraposición a ésto, *H. itala*, también con un comportamiento litoral en el área de estudio, no desciende del norte de Galicia, siendo su cita más al sur, en todo este territorio, la Sierra de O Courel, zona caliza con una altitud superior a los 900 m.

También hemos de señalar que la mayor parte de las especies han sido capturadas en gran variedad de hábitats (bajo troncos, muros, linderas de cultivos...), pudiendo destacar únicamente la preferencia de *E. quimperiana* por los diferentes tipos de arbolados, en mayor medida pinares y robledales, y de *P. inchoata* y *P. subvirescens* en los prados y zonas carentes de vegetación arborea.

Por último queremos mencionar que hemos encontrado la mayoría de las especies citadas anteriormente a nosotros en el área de estudio, y las que no lo han sido podemos atribuirlo, no tanto a errores de muestreo, como a la posibilidad de que se encuentren poco representadas. Este es el caso de *Helicigona lapicida* (Linneo, 1758) citada por ROLÁN y OTERO (1988) en una única localidad de la provincia de A Coruña. Así mismo, hay que señalar *Otala punctata* (Müller, 1771) citada como *Otala lactea* (Müller, 1771) por CASTILLEJO (1986) en la estación biológica de Lourizán (Pontevedra). Esta especie de ámbito mediterráneo fue, con seguridad, introducida con un cultivo experimental en la estación agrícola, y la población, muy abundante en el momento de su cita (el autor recoge unos 300 ejemplares) probablemente no prosperó, puesto que hemos realizado repetidas visitas a esa zona, sin encontrar ningún ejemplar.

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Una nueva especie de *Lirularia* (Gastropoda: Trochidae) de las islas de São Tomé y Príncipe, África Occidental

A new species of *Lirularia* (Gastropoda: Trochidae) from São Tomé y Príncipe Islands, West Africa

Federico RUBIO* y Emilio ROLÁN**

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RESUMEN

El estudio del material obtenido durante dos expediciones realizadas a las Islas de São Tomé y Príncipe en los años 1989 y 1990, ha proporcionado una nueva especie de tróquido con apariencia de *Solariella*, que por sus características morfológicas y radulares pertenece a la subfamilia Lirulariinae. Se describe esta especie, nueva para la ciencia, comentándose las características morfológicas de la concha, partes blandas y rádula, e incluyéndola en el género *Lirularia*. Se discute la inclusión en dicho género de otras dos especies de la costa occidental africana.

ABSTRACT

The study of the material obtained in São Tomé and Principe Islands during two expeditions in the years 1989 and 1990, have yielded a new trochid species with *Solariella*, which for its morphological and radular characters belongs to the subfamily Lirulariinae. This species is described as new for science within the genus *Lirularia* and its morphological characteristics of shell, soft parts and radula are commented on. The assignment to this genus of other two species of the West African coast is discussed.

PALABRAS CLAVE: Gastropoda, Trochidae, *Lirularia*, nueva especie, Islas de São Tomé y Príncipe.
KEY WORDS: Gastropoda, Trochidae, *Lirularia*, new species, São Tomé and Príncipe Islands.

INTRODUCCIÓN

Se han citado varias especies de *Solariella* s. l. de la costa africana en diversos trabajos. SMITH (1871) describe la primera, *Solariella canaliculata* Smith, 1871, de Whydah (Dahomey), actualmente República de Benin. Esta misma especie y *Solariella dereimsi* Dollfus, 1911 son citadas para Angola por GOFAS, PINTO AFONSO Y BRANDÃO (1985); NICKLÉS (1950) menciona *Solariella monodi* Fischer y Nicklés, 1946 para Guinea Francesa (Guinea Conakry) y *S. dereimsi* para Mauritania y Senegal. Alguna otra especie, como *S. valida* Dautzenberg y Fischer, 1906, descrita para el archipiélago de Cabo Verde, procede de aguas profundas.

En BERNARD (1984) aparece representada una concha con la denomina-

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ción *Solariella sp.*, pero en realidad se trata de *Cyclostremiscus calameli* (Jousseaume, 1872) que es en realidad un Tornidae (Gofas, com. pers.).

No hay citas de especies de *Solariella* para el archipiélago de São Tomé y Príncipe, aunque en el último listado de especies de FERNANDES Y ROLÁN (1993), se menciona una única especie de este género, como *Solariella* sp.

HERBERT (1987) demostró que muchas de las especies de África del Sur, consideradas tradicionalmente del género *Solariella* no lo son, sino que pertenecen a la subfamilia Umboniinae en lugar de Solariellinae. HICKMAN Y MCLEAN (1990) publicaron una revisión de la superfamilia Trochoidea y, atendiendo a la morfología de sus partes blandas y rádula, agruparon las *"Solariellas"* en un grupo informal formado por las subfamilias Trochinae Rafinesque, 1815, Stomatellidae Gray, 1840, Calliostomatinae Thiele, 1924 y Solariellinae Powell, 1951; agrupando las especies de Umboniinae en otro grupo informal formado por Lirulariinae Hickman y McLean, 1990, Halistylinae Keen, 1958 y Umboniinae Adams y Adams, 1854. WARÉN (1993), siguiendo dicha ordenación, considera que *"Solariella" canaliculata* y *"Solariella" dereimsi* pertenecen a la subfamilia Umboniinae.

Durante las campañas de recolección de moluscos efectuadas por el segundo autor en los años 1989 y 1990 en el archipiélago de São Tomé y Príncipe, Golfo de Guinea, se recolectaron ejemplares y conchas de una *"Solariella"* aparentemente diferente de las especies previamente conocidas. Esta misma especie, referida como *Solariella sp.* por FERNANDES Y ROLÁN (1993) y WARÉN (1993), es ahora descrita, aunque en un género diferente.

Al mismo tiempo, las *especies "Solariella" canaliculata* y *"Solariella" dereimsii,* recolectadas y observadas en las expediciones a Angola y Mauritania de 1989 y 1996 respectivamente, son transferidas a la subfamilia Lirulariinae, género *Lirularia,* basándonos en la similitud morfológica de sus partes blandas y rádula.

MATERIAL Y MÉTODOS

Se han estudiado 8 ejemplares y 82 conchas, procedentes de sedimentos obtenidos en distintas localidades del archipiélago, mediante buceo a pulmón libre, a profundidades comprendidas entre 5 y 15 metros. Tras la observación de su comportamiento, algunos individuos se relajaron y posteriormente se fijaron en solución tamponada de formaldehído al 5%. Para la observación conquiológica y radular se ha utilizado la microscopía electrónica de barrido.

RESULTADOS

Superfamilia TROCHACEA Rafinesque, 1815
Familia TROCHIDAE Rafinesque, 1815
Subfamilia LIRULARIINAE Hickman y McLean, 1990
Género *Lirularia* Dall, 1909

Lirularia antoniae spec. nov. (Figs. 1A-B, 2 - 6)

Material estudiado: Isla de São Tomé: Praia das conchas: 8 ejemplares y 16 conchas a -15 m; Ciudad São Tomé: 36 conchas. Isla de Príncipe: Bahía de Santo Antonio: 24 conchas a -10 m; Bahía das Agulhas: 6 conchas.

Material tipo: Holotipo (Fig. 1B) y dos paratipos procedentes de la localidad tipo, depositados en el Museo Nacional de Ciencias Naturales de Madrid, con el nº 15.05/23749, dos paratipos procedentes de Praia das Conchas (São Tomé) en el Muséum National d´Histoire Naturelle de París, dos paratipos procedentes de Ciudad de São Tomé en el American Museum of Natural History de Nueva York y en The Natural History Museum de Londres y 25 en cada una de las colecciones de los autores.

Localidad tipo: Praia das Conchas, São Tomé.

Etimología: La especie está dedicada a Antonia Hueso, esposa del primer autor.

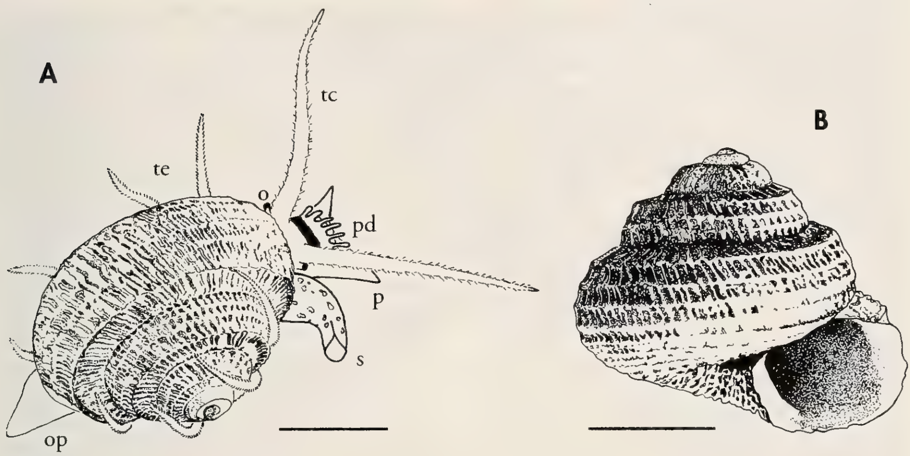


Figura 1. *Lirularia antoniae spec. nov.* Holotipo. Praia das Conchas, São Tomé. A: animal en movimiento. B: concha (MNCN). Escalas 1 mm.
Abreviaturas. o: ojo; op: opérculo; p: pie pd: proceso digitiforme sobre el extremo del morro; s: sifón; tc: tentáculo cefálico; te: tentáculo epipodial.
Figure 1. Lirularia antoniae *spec. nov. Holotype. Praia das Conchas, São Tomé. A: crawling animal. B: shell (MNCN). Scale bars 1 mm.*
Abbreviations. o: eye; op: operculum; p: foot; pd: digitiform processes on the tip of snout; s: siphon; tc: cephalic tentacle; te: epipodial tentacle.

Descripción: Concha sólida, brillante, nacarada, de perfil cónico y espira algo elevada, compuesta por unas 5 vueltas convexas, que están separadas por una sutura ancha y acanalada. Protoconcha (Fig. 5) con apenas una vuelta de espira, lisa, con el núcleo deformado y de unas 200 μm. Ornamentación formada por cordones espirales y costillas transversales muy numerosas, que al entrecruzarse forman pequeños nódulos; se observan, además, sutiles líneas de crecimiento que se extienden paralelas a las costillas. Última vuelta con 10 cordones espirales, de los que el primero, subsutural, y el décimo, periumbilical, son los más prominentes por ser nodulosos y angulan la concha. Los restantes cordones son poco marcados, sobre todo en la parte media de la periferia, donde apenas son perceptibles. Las costillas transversales están menos marcadas en la primera y última vuelta de la teloconcha, aunque en ésta última son numerosísimas; su curso es prosoclino y atraviesan la totalidad de la vuelta. Ombligo ancho y profundo, bordeado por el décimo cordón espiral; en su interior se observan otros cuatro cordones espirales más. Abertura subcircular, prosoclina; labio externo fino, angulado por la presencia de los cordones espirales; labio interno, ligeramente arqueado, reflejado hacia el exterior, pero sin llegar a ocluir el ombligo.

Coloración muy variable, de blanco-amarillento a rosa pálido, con manchas pardo rojizas o pardo oscuras y cierta iridiscencia.

Respecto a sus dimensiones, el holotipo (Fig. 1B) mide 1,78 mm de altura y 1,98 mm de anchura.

El animal (Fig. 1A) es de color blanquecino excepto el sifón y una franja de color negro situada en la parte distal del morro. La cabeza tiene un par de tentáculos cefálicos muy largos y con micropapilas, ojos negros situados sobre cortos pedúnculos y carece de membranas cefálicas. El morro está muy depri-

mido distalmente y sus extremos se prolongan transversalmente; hay un proceso digitiforme con forma de peine sobre su extremo. A cada lado de la cabeza se observa un lóbulo cervical modificado; el izquierdo, subdividido en apéndices tentaculiformes y, el derecho, que es plano, en el animal vivo, se enrolla para formar una estructura tubular con aspecto de sifón, moteado con manchas negro-opacas y de un tamaño similar a los tentáculos cefálicos. Epipodio con cuatro pares de tentáculos, carentes de macropapilas sensoriales en su base, el primer par en posición anterior y los tres pares restantes alrededor del lóbulo opercular. El pie es muy móvil, su extremo anterior es bilobulado y se prolonga lateralmente y luego se afila progresivamente hacia su extremo posterior, para acabar en punta.

Rádula (Fig. 6) formula N. 4. 1. 4. N. El diente central y los laterales son muy similares y están reducidos a láminas basales con una pequeña cúspide cada uno. El diente central está cubierto en parte por las láminas laterales más internas. Dientes marginales con cúspides relativamente largas y anchas, con dentículos romos y aserrados.

Distribución: Sólo conocida del archipiélago de São Tomé y Príncipe (Golfo de Guinea). No se han encontrado ejemplares de esta especie en zonas continentales próximas al archipiélago, por lo que, probablemente, se trata de un endemismo insular.

Hábitat: Especie infralitoral que vive sobre fondos de arena en zonas de aguas claras, entre -5 y -15 metros.

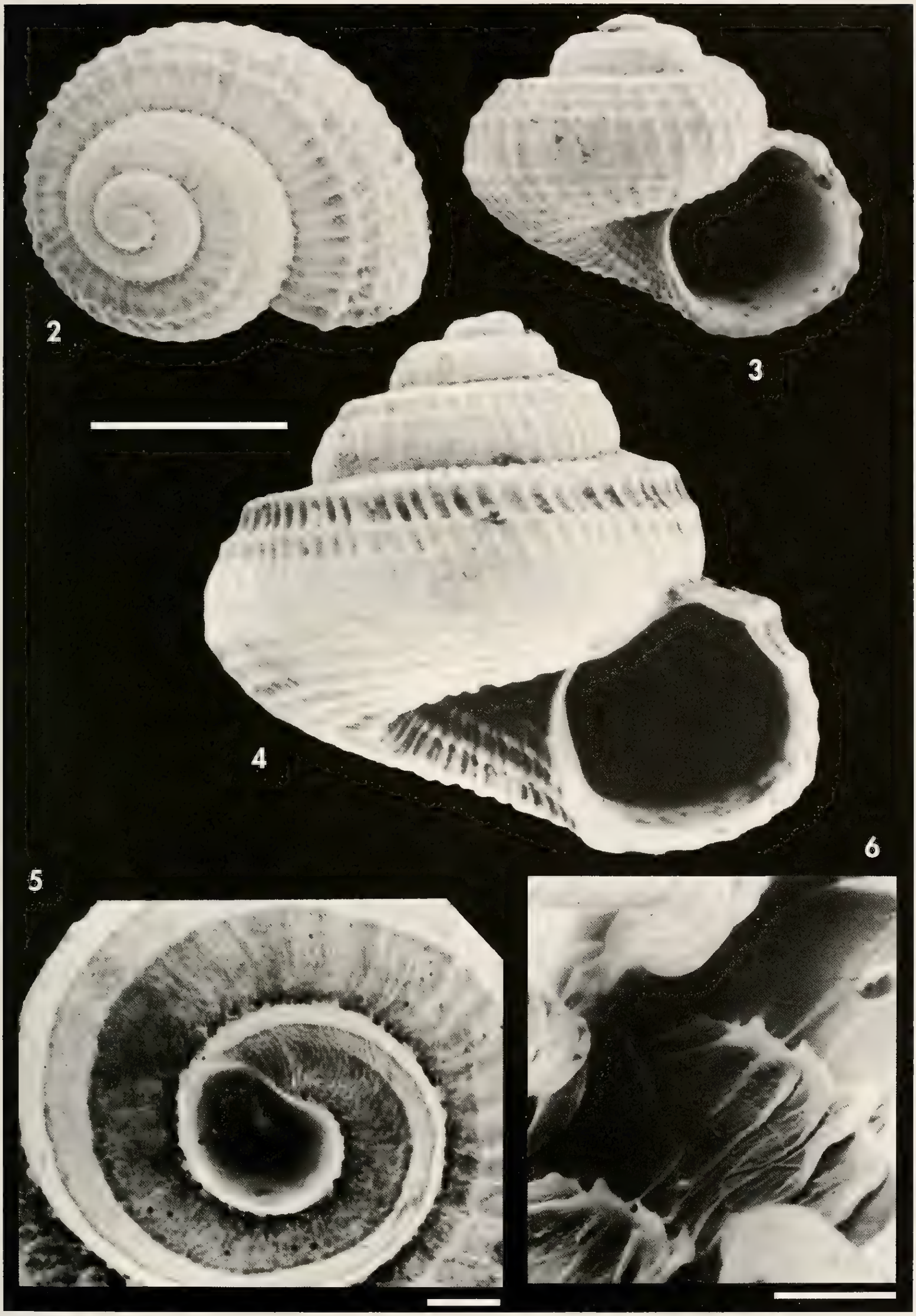
Discusión: Tanto la estructura plana, enrollada en forma de sifón, como los procesos digitiformes visibles a cada lado de la cabeza en *Lirularia antoniae*, al igual que en otras especies de África occidental (*"Solariella" canaliculata y "Solariella" dereimsii*) (Gofás com. pers.), son probablemente lóbulos cervicales modificados, homólogos a los de otros Trocoideos. Su función, para el lado inhalante, se puede suponer que es la de actuar como un filtro para evitar la entrada de las partículas en la cavidad paleal. El lóbulo derecho tiene una función exhalante. Dichas estructuras surgen como consecuencia de la adaptación de las especies de Solariellinae, Umboniinae y Lirulariinae de África occidental a los fondos blandos sobre los que habitan, a diferencia de otros trocoideos (*Clanculus, Collonia, Gibbula, Tricolia*, etc.) cuyo hábitat está limitado a fondos rocosos. Aspectos de esta adaptación coincidentes con estas características anatómicas pueden verse en FRETTER (1975) y HICKMAN (1985).

Siguiendo la clasificación de la familia Trochidae propuesta por HICKMAN Y MCLEAN (1990), y atendiendo a los caracteres morfológicos y radulares que diferencian las tres subfamilias que pertenecen al grupo informal Halistylinae + Umboniinae + Lirulariinae, hemos situado la nueva especie en la subfamilia Lirulariinae, género *Lirularia*. Las especies *"Solariella" canaliculata* (Fig. 7) y *"Solariella" dereimsii* (Figs. 8-9) son congenéricas entre sí, y se diferencian anatómicamente de *Lirularia antoniae* tan solo por la distribución de las papillas del morro; sin embargo, comparten caracteres comunes como:

- protoconchas de pequeño tamaño, no superior a 200 μm, con el núcleo deformado;
- ombligo amplio, no ocluido ni total ni parcialmente;
- radulas similares, muy parecidas a su vez a las de *Umbonium;*
- lóbulo cervical izquierdo subdividido en un proceso tentaculiforme y lóbulo cervical derecho plano, enrollado para formar una especie de sifón.

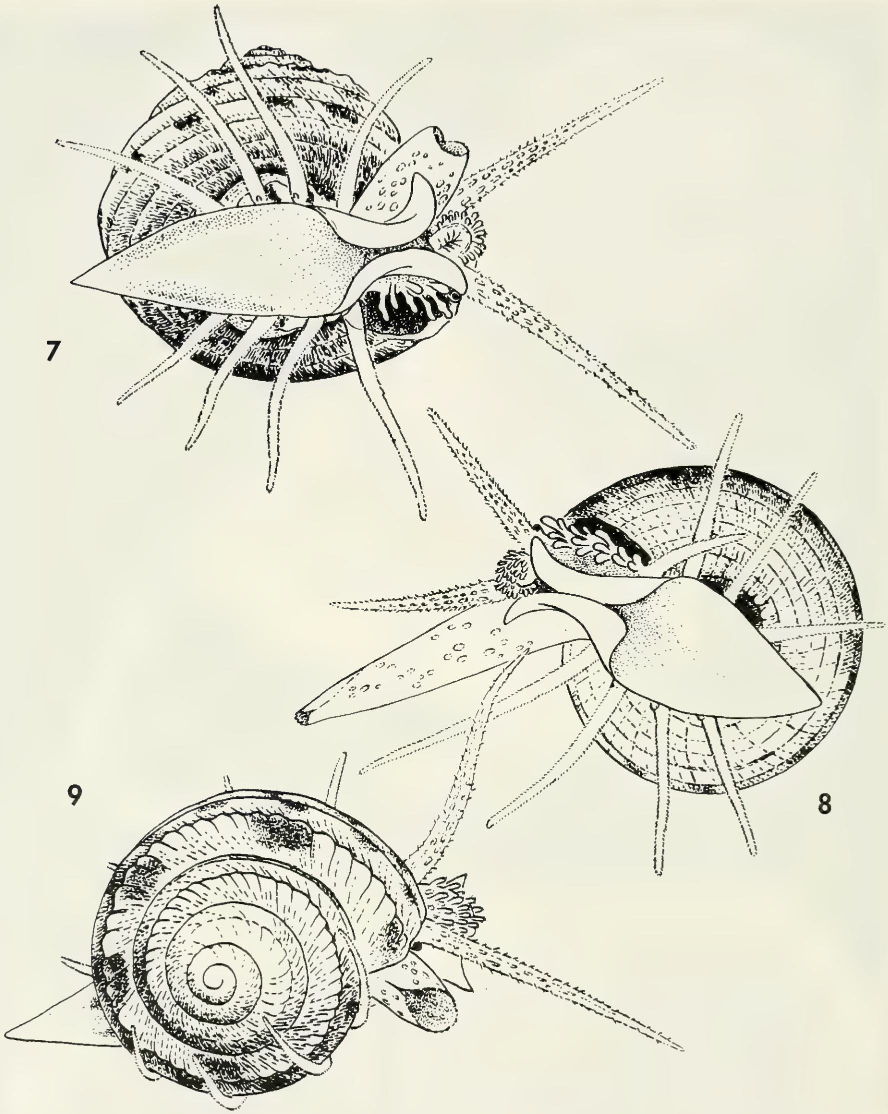
Todo esto nos hace considerarlas pertenecientes a la subfamilia Lirulariinae, género *Lirularia*, en lugar de Solariellinae o Umboniinae.

Lirularia antoniae, L. canaliculata y L. dereimsii, se diferencian de las especies pertenecientes a Solariellinae por tener protoconcha pequeña con el núcleo deformado, la rádula con su zona central simplificada, el diente central y los dien-



Figuras 2-6. *Lirularia antoniae* spec. nov., Praia das Conchas, São Tomé. 2: individuo juvenil, vista apical (col. F. Rubio); 3: individuo juvenil, vista dorsal; 4: paratipo (col. F. Rubio); 5: protoconcha; 6: rádula. Escalas, 2-4: 0,5 mm; 5: 100 µm; 6: 12 µm.

Figures 2-6. Lirularia antoniae *spec. nov., Praia das Conchas, São Tomé. 2: young specimen, apical view (F. Rubio coll.). 3: young specimen, dorsal view. 4: paratype (F. Rubio coll.); 5: protoconch; 6: radula. Scale bars, 2-4: 0,5 mm; 5: 100 µm; 6: 12 µm.*



Figuras 7-9. Animal de otras especies de *Lirularia* de Africa. 7: *L. dereimsii* (tomado de GOFAS, PINTO AFONSO Y BRANDÃO, 1985); 8-9: *L. canaliculata* (dibujo de S. Gofas).
Figures 7-9. Animal of other species of Lirularia *from Africa. 7:* L. dereimsii *(after GOFAS, PINTO AFONSO AND BRANDÃO, 1985); 8-9:* L. canaliculata *(drawing from S. Gofas).*

tes laterales reducidos, los tentáculos epipodiales carentes de macropapilas sensoriales en su base y las papilas situadas en el extremo anterior del morro y no alrededor del disco oral. De las especies pertenecientes a Umboniinae, tribu Umboniini se diferencian porque estas últimas poseen tentáculos cefálicos dimórficos y el lóbulo cervical izquierdo envuelve el tentáculo cefálico izquierdo y

pedúnculo ocular. De las especies pertenecientes a la tribu Monileini se diferencian porque presentan un ombligo cerrado, total o parcialmente, por un callo; por poseer pedúnculos oculares prominentes, con anchos ojos y bases desarrolladas; y porque su lóbulo cervical izquierdo (inhalante) está subdividido terminalmente en un proceso tentaculiforme dimórfico, orientado regular y alternativamente.

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Una nueva especie de *Anticlimax* (Gastropoda: Vitrinellidae) de Cuba

A new species of *Anticlimax* (Gastropoda: Vitrinellidae) from Cuba

Emilio ROLÁN*, Raúl FERNÁNDEZ-GARCÉS** y Federico RUBIO***

Recibido el 18-III-1996. Aceptado el 8-X-1996

RESUMEN

Se describe una nueva especie del género *Anticlimax* (Gastropoda: Vitrinellidae). Se discute su asignación genérica y se compara con las especies más próximas.

ABSTRACT

A new species of the genus *Anticlimax* (Gastropoda: Vitrinellidae) is described. Its generic assignment is discussed and a comparison is made with allied species.

PALABRAS CLAVE: Gastropoda, Vitrinellidae, *Anticlimax*, especie nueva, Cuba.
KEY WORDS: Gastropoda, Vitrinellidae, *Anticlimax*, new species, Cuba.

INTRODUCCIÓN

DALL (1903) menciona por primera vez el subgénero *Climacia* en la descripción de *Teinostoma* (*Climacia*) *calliglyptum*, sin hacer descripción alguna de las características del subgénero ni de las de la especie típica, siendo ambos definidos por figuras (PILSBRY Y MCGINTY, 1946a).

PILSBRY Y MCGINTY (1946a) dan a *Climacia* categoría genérica y describen y comentan las características de *T. calliglyptum* como las de la especie típica (por monotipia); al tiempo describen varias especies nuevas que incluyen en *Climacia*.

AGUAYO Y BORRO (1946) sustituyen por *Climacina* el previamente ocupado nombre genérico de *Climacia* Dall, 1903 *non* M'Lachlan, 1869 (Neuroptera). Poco tiempo después, PILSBRY Y MCGINTY (1946b) sustituyen *Climacina* Aguayo y Borro, 1946 *non* Gemmellaro, 1878 (Mollusca), por un nuevo nombre: *Anticlimax*.

PILSBRY Y OLSSON (1950) hacen una revisión del género describiendo algunas especies nuevas del Terciario americano, y lo subdividen en dos subgéneros *Anticlimax* y *Subclimax* subgen. nov.

En el material recolectado en Cuba durante los muestreos realizados por los dos primeros autores en los últimos años, se han encontrado conchas de una especie que parece pertenecer a este género, y que es descrita en el presente trabajo.

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RESULTADOS

Género *Anticlimax* Pilsbry y McGinty, 1946

Especie tipo, por monotipia: *Teinostoma* (*Climacia*) *calliglyptum* Dall, 1903

Anticlimax decorata spec. nov.

Material tipo: Holotipo, de Rancho Luna, Cienfuegos, Cuba (Fig. 2), con 1,3 mm de dimensión máxima, Museo Nacional de Ciencias Naturales de Madrid nº 15.05/27420. De la misma localidad, un paratipo en las colecciones del American Museum of Natural History de Nueva York (Fig. 1) y The Natural History Museum de Londres y dos en la de R. Fernández Garcés. Zona del Hotel Comodoro, La Habana, Cuba: un paratipo en la colección del Instituto de Ecología y Sistemática de La Habana. Jibacoa, Distrito de La Habana, Cuba: un paratipo en la colección de F. Rubio y otro en la de E. Rolán.
Localidad tipo: Rancho Luna, Cienfuegos, Cuba.
Etimología: El nombre específico deriva de su elaborada escultura.

Descripción: Concha (Figs. 1 y 2) discoidal algo ovalada, aplanada en la base y con el ápice apenas saliente, espira con elevación uniforme, suavemente convexa y no muy pronunciada. Color blanquecino.

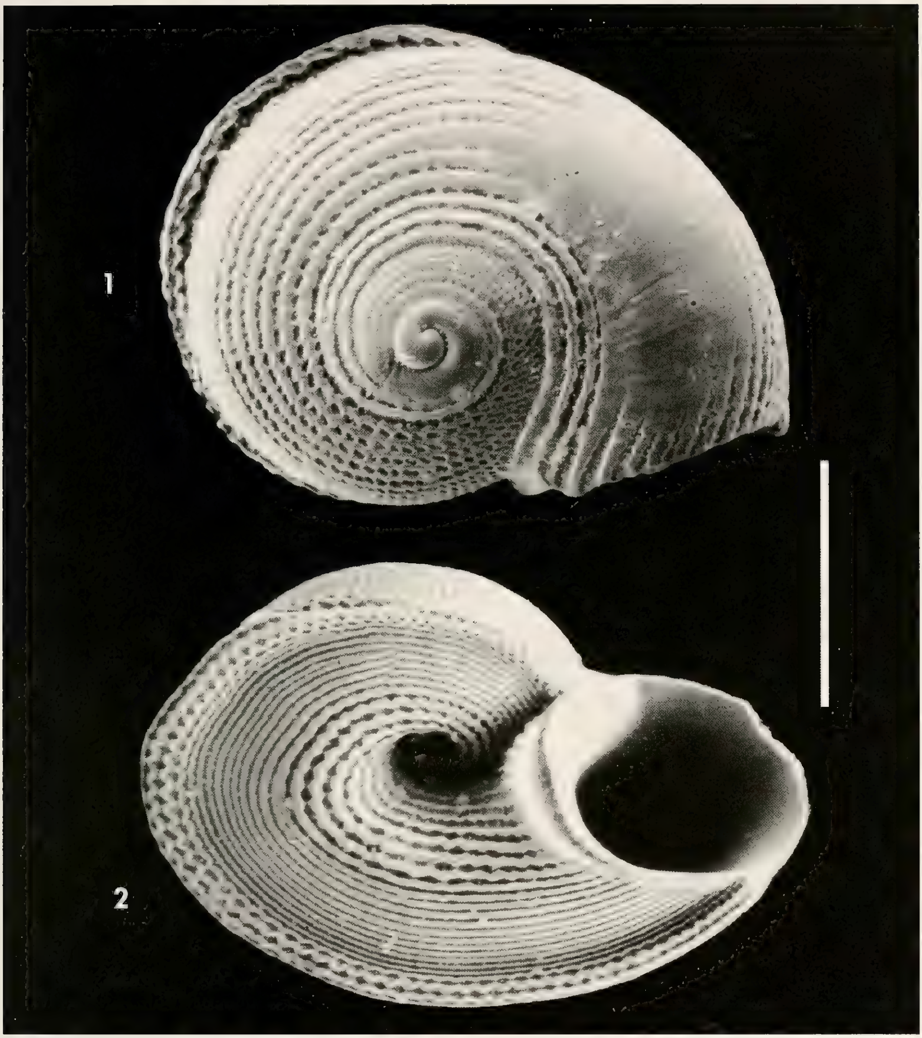
Protoconcha lisa con $1^1/_4$ vueltas de espira. Termina bruscamente y de forma bien delimitada con la teloconcha.

Teloconcha formada por $1^3/_4$ vueltas. La microescultura es compleja: al final de la última vuelta hay tres cordones espirales en posición subsutural, de los cuales, los dos primeros se inician de forma progresiva, mientras el tercero se origina por una división del segundo. El resto de la superficie presenta surcos bastante uniformes constituidos, al principio, por perforaciones y, posteriormente, por hundimientos de forma más alargada. Esta escultura desaparece casi por completo en el último cuarto de vuelta de forma muy constante. Hacia la parte inferior de la última vuelta la concha se angula y se hace prominente por medio de un grueso cordón que sobresale del perfil de la concha a modo de quilla y sobre el cual aparecen varios cordoncillos en zigzag. Este cordón, visto desde la parte superior de la concha, es más visible por un lado que por el otro, lo que aumenta el perfil ovoide de la concha. La parte de la última vuelta que está por debajo de la angulación apenas sobrepasa al cordón periférico y es cóncava en la proximidad del mismo. En su parte central hay un ombligo profundo. Toda la base presenta cordoncillos espirales; los que bordean el ombligo son gruesos y zigzagueantes, y lo mismo ocurre con los que se sitúan sobre la quilla, siendo los restantes algo más finos y uniformes.

Abertura circular, con borde fino, engrosado en su parte externa por el final del cordón espiral sobresaliente.

El animal es desconocido.

Discusión: La especie ahora descrita es incluida en el género *Anticlimax* como una aproximación, ya que presenta algunas diferencias con la especie tipo. Estas diferencias son, principalmente, la carencia de escultura axial en la base y la ausencia de una prolongación de la abertura en la finalización del cordón espiral. Sin embargo, la subespecie *A. tholus prodromus* Pilsbry y Olsson, 1950, apenas presenta escultura axial en la base y también carece de la prolongación de la abertura, habiendo sido no obstante incluida en este género. *A. decorata* spec. nov., además de parecerse a esta última especie, tiene muchas de sus características coincidentes con especies que han sido consideradas pertenecientes al género *Anticlimax*, como la base aplanada o cóncava, el cordón periférico, la superficie convexa por encima del mismo, la existencia de cordones en



Figuras 1, 2. *Anticlimax decorata* spec. nov. 1: paratipo, Rancho Luna, Cienfuegos, Cuba, American Museum of Natural History de Nueva York; 2: holotipo, Rancho Luna, Cienfuegos, Cuba, Museo Nacional de Ciencias Naturales de Madrid. Escala 0,5 mm.
Figures 1, 2. Anticlimax decorata *n. sp. 1: paratype, Rancho Luna, Cienfuegos, Cuba, American Museum of Natural History, New York; 2: holotype, Rancho Luna, Cienfuegos, Cuba, Museo Nacional de Ciencias Naturales, Madrid. Scale bar 0.5 mm.*

el dorso formados por perforaciones, y los cordones en zigzag de la base.

Su parecido con *A. athleenae* (Pilsbry y McGinty, 1946) es bastante notable, aunque esta especie se diferencia de *A. decorata* porque presenta ondulaciones en la base, y carece, tanto en la base como en el cordón periférico, de cordoncillos en zigzag. Tambien con *A. tholus* (Pilsbry y McGinty, 1946) tiene un cierto parecido, pero el ombligo de esta última está ocluido por un fuerte callo.

Las restantes especies incluidas en este género, o tienen escultura axial, o el

ombligo está ocluido por un callo, o tienen una prolongación triangular en la abertura como continuación de la quilla periférica, por lo que son claramente diferentes de *A. decorata*.

Según ESPINOSA, FERNÁNDEZ-GARCÉS Y ROLÁN (1995), para la fauna de Cuba, únicamente era conocida una especie en el género *Anticlimax*: *A. proboscidea* (Aguayo, 1949), la cual es más elevada y tiene una gran prolongación de la abertura.

La principal diferencia entre los dos subgéneros, *Anticlimax* y *Subclimax*, en los que PILSBRY Y OLSSON (1950) dividieron las especies del género *Anticlimax* es que, en el primero, el ombligo es evidente mientras que, en el segundo, existe un callo columelar que cubre parcial o totalmente el ombligo. Estos autores mencionan que no conocen especies de estructura intermedia entre ambos subgéneros. *Anticlimax decorata*, por su ombligo abierto y carencia de callo columelar, no estaría incluida en el subgénero *Subclimax*; pero por la carencia de cualquier tipo de prolongación triangular en la abertura, tampoco presentaría perfectamente las características del subgénero *Anticlimax*. Por tanto, *Anticlimax decorata* representa una forma intermedia entre ambos subgéneros.

En cualquier caso, en ausencia de información sobre las partes blandas, es preferible no asumir su posición taxonómica genérica más que como probable y no hacer uso de asignación subgenérica alguna.

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La familia Pyramidellidae Gray, 1840 (Mollusca, Gastropoda) en África occidental. 1. El género *Sayella* Dall, 1885

The family Pyramidellidae Gray, 1840 (Mollusca, Gastropoda) in West Africa. 1. The genus *Sayella* Dall, 1885

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RESUMEN

Se describen dos especies nuevas del género *Sayella* Dall, 1885 de África Occidental, una de ellas encontrada en los Archipiélagos de Cabo Verde y de São Tomé y Príncipe, y otra, sólo en el segundo de ellos.

ABSTRACT

Two new species of the genus *Sayella* Dall, 1885 from West Africa are described; one of them found in the archipelagos of Cape Verde, and São Tomé and Principe, the other one only in the latter.

PALABRAS CLAVE: Pyramidellidae, *Sayella*, África occidental, especies nuevas.
KEY WORDS: Pyramidellidae, *Sayella*, West Africa, new species.

INTRODUCCIÓN

Después de realizada la revisión de los piramidélidos del Mediterráneo ibérico (PEÑAS, TEMPLADO Y MARTINEZ, 1996) y animados por los recientes trabajos de NOFRONI Y SCHANDER (1994) y SCHANDER (1994), en los que se describen 31 especies nuevas de este grupo en África occidental, unido a la gran cantidad de material que poseemos, nos decidió a abordar el estudio de esta familia en las costas atlánticas africanas. Comenzamos esta revisión con el género *Sayella* Dall, 1885, hasta ahora no mencionado en el área geográfica de estudio, y continuaremos de forma inmediata con la de los géneros *Turbonilla, Eulimella, Chrysallida* y otros.

El género *Sayella* fue descrito por DALL (1885) para una especie fósil del Mioceno y bajo Plioceno de Louisiana. Inicialmente, la especie tipo, *Leuconia hemphillii* Dall, 1884, fue incluida por su autor en la familia Ellobiidae (Pulmonata). *Sayella* no aparece mencionado en las revisiones genéricas de THIELE (1931-35) o de WENZ (1938). La posición de este género y sus relaciones con otros Pyramidellidae son discutidas por ODE (1994), que comenta sus diferencias con *Odostomia* y la dificultad para la separación de especies, revisando también los taxones del Atlántico occidental. Las características del género son referidas por ABBOTT (1974) como "concha pu-

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poide-alargada, frágil, lisa, con vueltas convexas. Animal con tentáculos aplanados, triangulares. Periostraco amarillento". Se ha señalado en aguas someras y fondos fangosos (ABBOTT, 1974).

Recientemente, WISE (1996), basándose en datos anatómicos, crea la subfamilia Sayellinae para incluir a las especies de este género. Asimismo, describe para la especie *S. crosseana* (Dall, 1885) un nuevo género, *Petitiella*, por sus diferencias anatómicas, al que también incluye en esta subfamilia.

En el presente trabajo abordamos la descripción de dos especies que consideramos nuevas y que asignamos provisionalmente a *Sayella*, pués carecemos de los datos anatómicos necesarios para confirmar su pertenencia a este género. Dado el escaso número de vueltas de su protoconcha, cabe pensar que estas especies carecen de un desarrollo larvario plantotrófico, y que, por tanto, es poco probable una relación estrecha con especies del Atlántico occidental. Dicho género no ha sido mencionado con anterioridad en las costas occidentales de África.

MATERIAL Y MÉTODOS

El material estudiado en el presente trabajo procede de las expediciones efectuadas por el segundo de los autores al archipiélago de Cabo Verde entre los años 1978 y 1988, y a São Tomé y Príncipe en los años 1989 y 1990. Dicho material fue separado de los detritos recogidos mediante buceo y dragado.

Abreviaturas empleadas:

AMNH: American Museum of Natural History, New York
BMNH: The Natural History Museum, Londres
CER: Colección de E. Rolán
CPM: Colección de P. Micali
MNCN: Museo Nacional de Ciencias Naturales, Madrid
MNHN: Museum National d'Histoire Naturelle, Paris

RESULTADOS

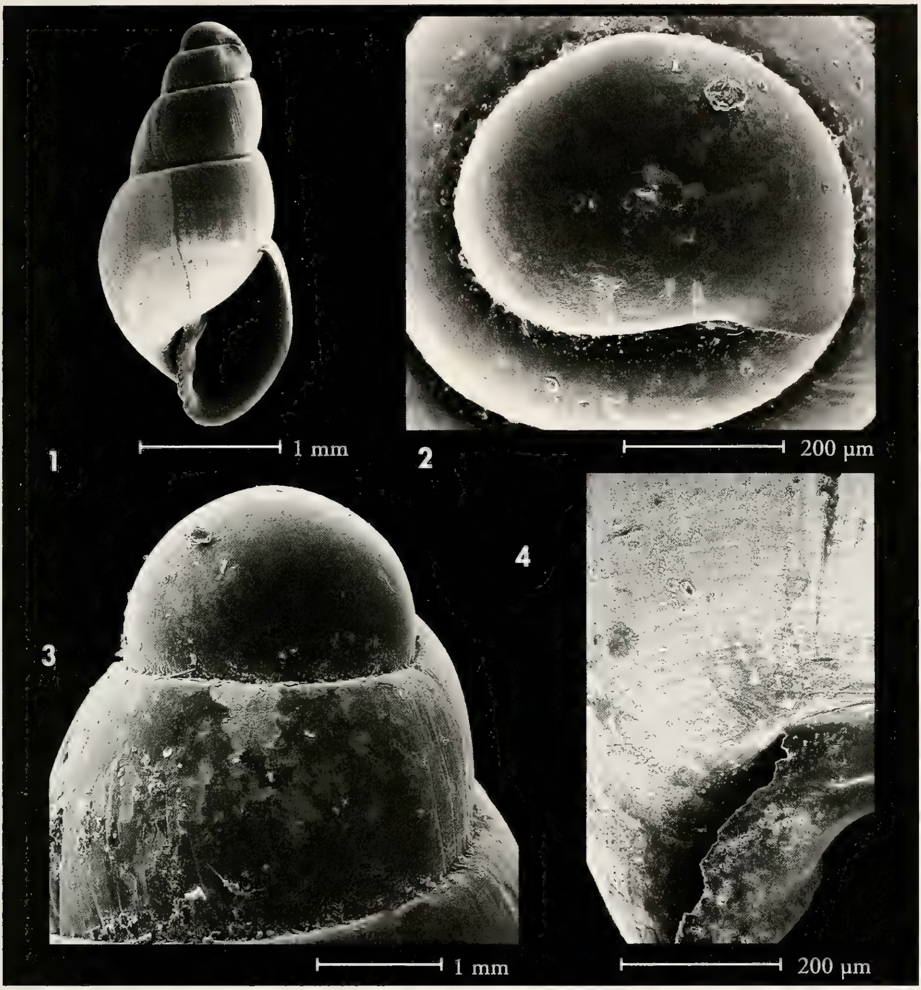
Familia PYRAMIDELLIDAE Gray, 1840
Subfamilia SAYELLINAE Wise, 1996

Género *Sayella* Dall, 1885

Las características del género *Sayella* son: concha pequeña, pupoide alargada, vueltas lisas, sutura poco profunda, bandas espirales de color, protoconcha corta con núcleo oculto, y periostraco acastañado.

Sayella micalii spec. nov. (Figs 1-5)

Material tipo: Holotipo (Fig. 1) de 2,86 x 1,35 mm depositado en MNCN (nº 15.05/23757) y 1 paratipo, ambos de la Bahía de Santo Antonio, Príncipe, República de São Tomé y Príncipe. Otros paratipos en las siguientes colecciones: MNHN, 1 concha y dos juveniles de Bahía das Agulhas, Príncipe; BMNH, 1 concha, y AMNH, 1 concha, ambas a -10 m, de Regona, Isla de Sal, Archipiélago de Cabo Verde; CPM, 1 concha, -8 m, de Furna, Isla de Brava, Archipiélago de Cabo Verde; CER, 1 concha, -2 m, de la ciudad de São Tomé, República de São Tomé y Príncipe y otra, -10 m, de Furna, Isla de Brava, Cabo Verde.
Localidad tipo: Bahía de Santo Antonio, en la isla de Príncipe, Archipiélago de São Tomé y Príncipe.
Etimología: El nombre específico está dedicado al malacólogo Pasquale Micali, experto en Pyramidellidae del Mediterráneo, por su habitual cooperación en el estudio de estos moluscos.



Figuras 1-4. *Sayella micalii* spec. nov. 1: holotipo (MNCN), Bahía de Santo Antonio, Príncipe, Archipiélago de São Tomé y Príncipe; 2, 3: protoconcha; 4: detalle de la columela y de la microescultura.
Figures 1-4. Sayella micalii *n. sp. 1: holotype (MNCN), Santo Antonio Bay, Principe, Archipelago of São Tomé and Principe; 2, 3: protoconch; 4: detail of the columela and microesculpture.*

Descripción: Concha (Figs. 1 y 5) oval-cónica, muy frágil.

Protoconcha (Figs. 2 y 3) obtusa, muy grande, de tipo B (según Aartsen, 1981), con un diámetro de 490 μm. Eje con un ángulo de unos 100° en relación al de la teloconcha, y núcleo parcialmente oculto. Coloración castaña clara.

Teloconcha con vueltas convexas, algo escalonadas, que crecen deprisa; la última vuelta es muy grande, representando un 60% del total de su altura. Sutura profunda con una débil repisa subsutural. Vueltas de espira lisas, excepto débiles líneas de crecimiento ligeramente prosoclinas y estrías microscópicas espirales, más visibles en la zona umbilical (Fig. 4).

Abertura grande, oval alargada, con un labio externo simple, cortante. Columela ligeramente arqueada, delgada, pero muy replegada hacia la zona umbilical; tiene dos dientes, el mayor muy saliente

y situado en la parte superior de la columela; el segundo en la parte central, en forma de cordoncillo oblícuo. Fisura umbilical profunda. Color vítreo, semitransparente, con una banda suprasutural castaña y otra en la base de la última vuelta, en la que también se aprecia otra banda subsutural (Fig. 5). Periostraco amarillento.

Distribución: Conocida únicamente de los Archipiélagos de Cabo Verde y São Tomé y Príncipe.

Hábitat: En sedimentos de arena y fango, entre 4 y 10 m de profundidad.

Discusión: No hay ninguna especie similar a *Sayella micalii* spec. nov. en el Mediterráneo ni en las costas de África occidental. Todas las especies del Caribe asignadas a este género (ver Abbott, 1974) son diferentes porque tienen más vueltas de teleoconcha, con un incremento más lento de la espira y una forma más lanceolada que cónica.

Sayella mercedordae spec. nov. (Figs. 6-8)

Material tipo: Holotipo (Fig. 7) de 2,10 x 0,90 mm depositado en MNCN (nº 15.05/23758); 1 paratipo (Fig. 6) de Rife de Chaves, Boavista, en CER.
Localidad tipo: Bahía de Mordeira, en la isla de Sal, Archipiélago de Cabo Verde.
Etimología: El nombre específico está dedicado a Mercedes Dorda, esposa del malacólogo Esteban Calderón, por su colaboración a lo largo de toda su vida en la creación y mantenimiento de su colección.

Descripción: Concha (Figs. 6 y 7) oval-cónica, pequeña, y frágil.

Protoconcha (Figs. 8) pequeña, de tipo B, tendente a C (de acuerdo con Aartsen, 1981). Su eje forma un ángulo de unos 100° en relación al de la teloconcha. Núcleo oculto.

Teloconcha con vueltas convexas, que crecen deprisa en altura y anchura. La última vuelta es muy grande, representando un 70% del total de la altura de la concha. Sutura muy marcada, algo profunda. Vueltas de espira lisas, exceptuando líneas de crecimiento ligeramente prosoclinas y estrías microscópicas espirales en la base.

Abertura oval-piriforme, estrechada hacia arriba. Columela opistoclina, algo arqueada, sin un diente claro, pero con un pliegue columelar en su parte central. No hay ombligo. Color blanquecino con dos estrechas bandas de color pardo por vuelta, y otra más, del mismo color, próxima a la zona columelar (Fig. 8).

Distribución: Conocida únicamente del Archipiélago de Cabo Verde.

Hábitat: Fondos arenosos entre 3 y 5 metros de profundidad, con zonas de fango próximas.

Discusión: *Sayella micalii* spec. nov., es mucho grande, ancha, con forma más piramidal y con protoconcha mucho más gruesa.

Las especies del Caribe son todas de mayor tamaño; *Sayella fusca* (C. B. Adams, 1839) tiene la sutura menos profunda y una banda clara subsutural; *S. livida* Rehder, 1935, tiene también una banda clara subsutural y un mayor número de vueltas de espira; *S. crosseana* (Dall, 1885) es mucho más alargada y proporcionalmente más estrecha; *S. hemphilli* (Dall, 1889) y *S. chesapeakea* Morrison, 1939, tienen la sutura apenas marcada y un número mayor de vueltas de espira.

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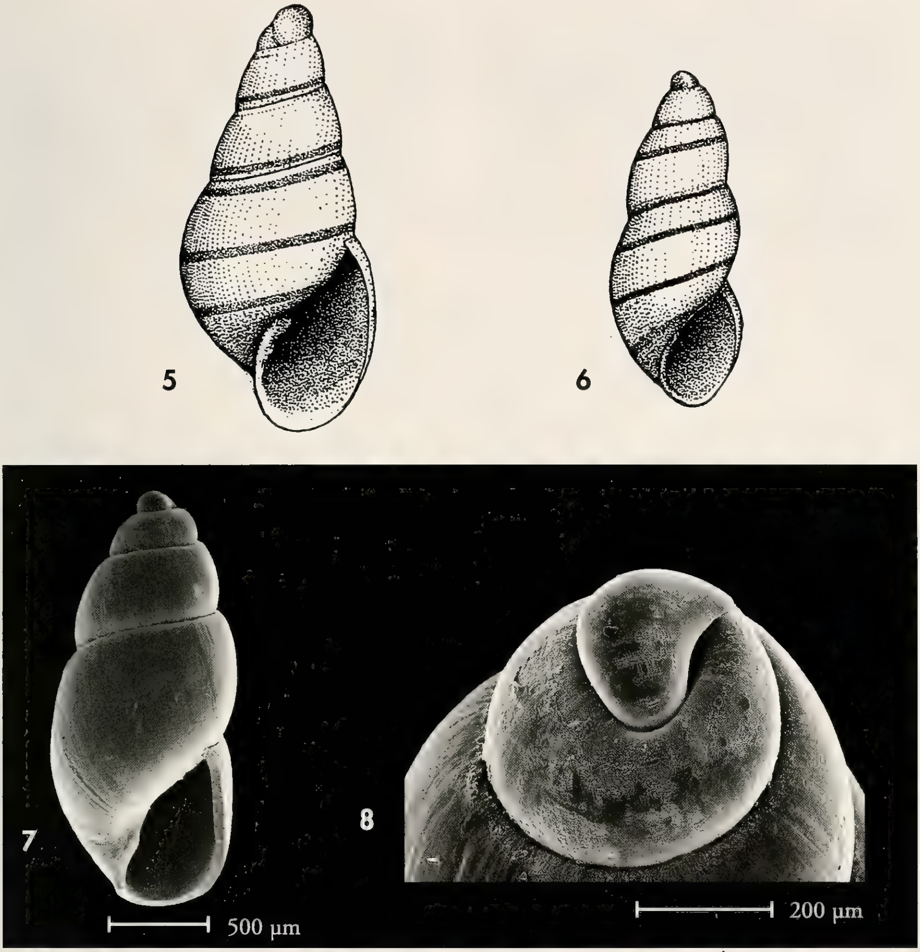

Figura 5. *Sayella micalii* spec. nov. Dibujo del paratipo (CER) mostrando la distribución de las bandas de color. Figuras 6-8. *S. mercedordae* spec. nov. 6: dibujo de un paratipo (CER) mostrando la distribución de las bandas de color; 7: holotipo (MNCN), Bahía de Mordeira, Isla de Sal, Archipiélago de Cabo Verde; 8: protoconcha.
Figure 5. Sayella micalii *n. sp. Drawing of paratype (CER) showing the distribution of the colour bands. Figures 6-8.* S. mercedordae *n. sp. 6: drawing of a paratype (CER) showing the distribution of the colour bands; 7: holotype (MNCN), Mordeira Bay, Sal Island, Archipelago of Cape Verde; 8: protoconch.*

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Fauna malacológica del litoral del Garraf (NE de la Península Ibérica)

Malacological marine fauna from Garraf coast (NE Iberian Peninsula)

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RESUMEN

Se presenta una lista de 622 especies de moluscos marinos (7 Poliplacóforos, 417 Gasterópodos, 190 Bivalvos y 8 Escafópodos) recolectados en el litoral del Garraf (Barcelona, NE de la Península Ibérica). De estas especies, 53 se citan por primera vez en el Mediterráneo español, siendo dos de ellas primera cita para todo el Mediterráneo, *Trophon barvicensis* y *Pleurotomella coeloraphe*. De particular interés ha resultado el estudio de un nuevo yacimiento de sedimentos Würmienses, asociado a una biocenosis de corales blancos, entre 250 y 350 m de profundidad, y el análisis del contenido gástrico de unos tres mil ejemplares de estrellas de mar del género *Astropecten*, recolectadas entre 40 y 350 m de profundidad. Se incluyen, asimismo, comentarios sobre algunos de los taxones mencionados y se ilustran al MEB muchos de ellos, con especial atención a los de las familias Cerithiopsidae, Turridae de profundidad, Yoldiidae y Thyasiridae.

ABSTRACT

We report a checklist of 622 marine molluscs (7 Poliplacophors, 417 Gastropods, 190 Bivalves and 8 Scaphopods) from "El Garraf" coast (Barcelona, NE Iberian Penninsula). From these species, 53 are new findings for the Spanish Mediterranean, and two of them, *Trophon barvicensis* and *Pleurotomella coelorophe*, are reported for the first time for the whole Mediterranean. A new Würm bed associated with a white coral biocenosis has been found off Vallcarca at depths between 250 and 350 m, and is described here. Data about molluscs identified from the gut contents of about 3000 specimens of *Astropecten* sea stars found between 40 and 350 m depth are also reported. Also, we include comments about some of the listed taxa and a special SEM image collections, particularly of such groups as Cerithiopsidae, deep-sea Turridae, Yoldiidae and Thyasiridae.

PALABRAS CLAVE: Moluscos marinos, Garraf, NE Península Ibérica, Mar Mediterráneo, tanatocenosis Würmiense, biocenosis de coral blanco, contenidos estomacales de *Astropecten*.
KEY WORDS: Marine molluscs, Garraf, NE Iberian Penninsula, Mediterranean Sea, Würm tanatocenosis, white coral biocenosis, *Astropecten* gut contents.

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INTRODUCCIÓN

El presente trabajo trata sobre los moluscos marinos (exceptuando la Clase Cephalopoda) que se han encontrado en el litoral de la comarca del Garraf (Barcelona) durante más de una década de recolección y estudio de material. Aunque, aparentemente, la región objeto de estudio no presente ninguna particularidad biogeográfica o física que la delimite desde un punto de vista biológico, la consideramos de especial interés, puesto que en un área relativamente pequeña se encuentran representados buena parte de los ecosistemas marinos del Mediterráneo. Ésto se refleja en la gran diversidad de especies encontrada en esta zona. Otro factor importante que determina la riqueza faunística del Garraf es la existencia de diferentes tipos de fondos, con numerosos cañones submarinos, por lo que a sólo 14 km del puerto principal (Vilanova i la Geltrú) se alcanzan profundidades de unos 530 m, mientras que en otras zonas próximas la distancia se triplica para llegar a profundidades semejantes.

Varios autores han estudiado la fauna malacológica marina de esta comarca (SAMÀ, 1916; HIDALGO, 1917; VILELLA, 1968; ROS, 1975; BALLESTEROS 1977, 1978 Y 1984; ASENSI, 1984), que ha ofrecido una gran riqueza en cuanto a número de especies, pero en ninguno de los casos anteriores se habían muestreado todos los hábitats encontrados en este litoral, o al menos no se había hecho de una forma tan extensiva. Ya HIDALGO (1917) citaba para la zona de estudio 307 especies de moluscos (191 Gasterópodos, 108 Bivalvos, 4 Escafópodos y 1 Cefalópodo), y SAMÀ (1916) citaba 319 especies y 81 variedades.

ZONA DE ESTUDIO

El Garraf es una pequeña comarca litoral situada al sur de Barcelona (Fig. 1), en cuyo interior se encuentra el Parque Natural del Garraf. Los aproximadamente 25 km de costa que presenta esta comarca, están comprendidos entre la desembocadura del río Foix (41° 12′ N, 1° 40′ E) y punta Ginesta (41° 16′ N, 1° 57′ E). Tres son los municipios litorales que se encuentran: Sitges, Vilanova i la Geltrú, y Cubelles, incluyendo el primero de ellos las pedanías de Garraf y Vallcarca. La existencia del importante puerto pesquero de Vilanova i la Geltrú, así como la colaboración de algunos de los pescadores de su cofradía, han sido factores decisivos para proporcionarnos gran parte del material en el que está basado este estudio.

Las playas de arena fina con pendientes poco pronunciadas son dominantes en la zona, aunque antes de la construcción generalizada de espigones, había algunas calas de arenas gruesas con pendientes más pronunciadas, como Cala Morisca (en Vallcarca) o Aiguadolç (en Sitges). Los fondos de arena fina son el hábitat típico de algunos Nassariidae, Naticidae y varios bivalvos, sobre todo de las especies de aguas someras de las familias Tellinidae, Pharidae, Donacidae, Veneridae, Mactridae, Pandoridae y Thraciidae. También se encuentran gran cantidad de escolleras o espigones, que están proliferando por toda la zona, tanto para la creación de puertos deportivos, como para formar playas artificiales.

Además son importantes las paredes rocosas de los acantilados calcáreos típicos del macizo del Garraf, que emergen casi verticalmente de fondos arenosos desde profundidades comprendidas entre 0, 5 y 4 m. Estas rocas son poco ricas desde el punto de vista malacológico, aunque presentan grandes bancos de *Mytilus galloprovincialis* (Linnaeus, 1758), y pueden llegar a abundar especies como *Thais haemastoma* (Linnaeus, 1767) y, sobre todo por encima de la línea de marea, algunas especies de los géneros *Patella, Gibbula* o *Littorina.*

La desembocadura de algunas rieras de cauce intermitente son muy interesantes desde el punto de vista faunístico. Este es el caso de la riera de Vila-

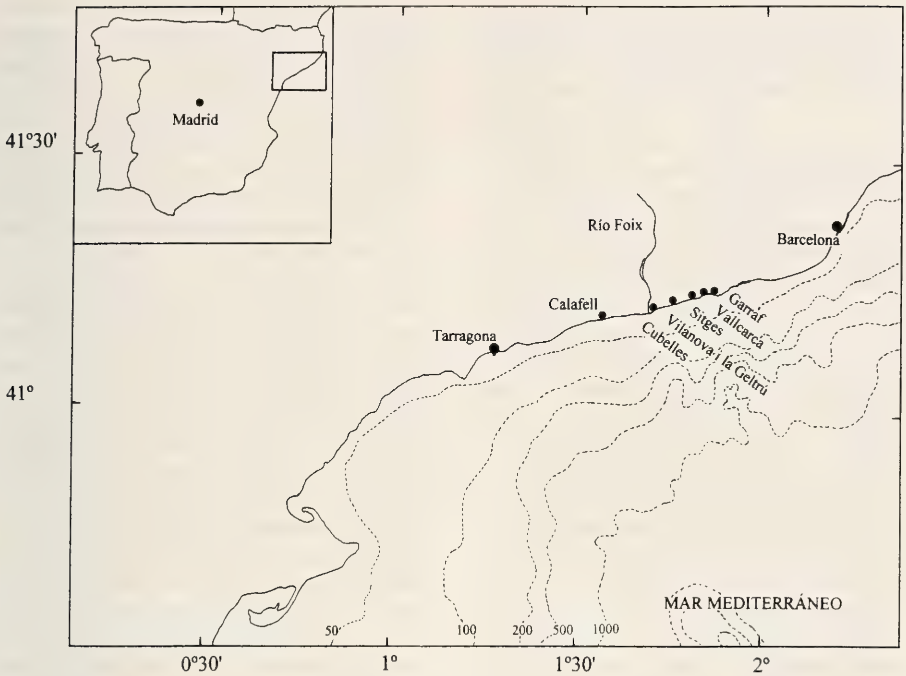


Figura 1. Mapa de la zona estudiada.
Figure 1. Map of studied area.

franca, que desemboca al sur de Sitges, y especialmente la desembocadura del río Foix en Cubelles. Esta última zona está formada por una base de arena fina, casi fangosa, rica en sedimentos orgánicos, cubierta casi completamente por cantos rodados y piedras aportadas esporádicamente por el río (suele estar seco por la presencia de una presa de contención situada unos kilómetros más arriba), que sólo lleva agua en forma de grandes avenidas. La profundidad máxima en esta zona de cantos rodados es de aproximadamente 1 m, y a partir de aquí ya se encuentra el típico fondo arenoso que caracteriza a las playas circundantes. La base pedregosa presenta una gran riqueza malacológica, principalmente de Opistobranquios. Esta zona concreta de Cubelles ha sido previamente estudiada por ROS (1975) y, principalmente, por BALLESTEROS (1977, 1978 y 1984), y constituye la localidad tipo de *Taringa faba* (Ballesteros, Llera y Ortea, 1984). Una buena descripción del recubrimiento algal así como de la fauna de Invertebrados acompañante se puede encontrar en BALLESTEROS (1984).

Situada paralelamente a la costa y a una distancia media de ésta de aproximadamente 2, 5 km, se encuentra una pradera de *Posidonia oceanica* (L.) Dellile. Hace unos 25 años, esta pradera de fanerógamas era muy densa y extensa, encontrándose desde los 8 m de profundidad (frente a Terramar, en Sitges) hasta 22 m en algunos puntos, y su longitud era de unos 10 km de largo por casi 2 km de anchura. Esta pradera ha sufrido una regresión considerable durante las dos últimas décadas, y con ella muchas de las especies típicas de estos hábitats, como *Pinna nobilis* Linnaeus, 1758, muy común anteriormente, y que ya prácticamente no se encuentra viva en esta comarca litoral.

Los fondos de aguas profundas se dividen en "La Mar de Terra" y "La Mar de Fora", que están separadas por una serie de rocas dispuestas paralelamente a la costa. "La Mar de Terra" es una planicie fangosa con una profundidad máxima que oscila entre los 74 y los 105 m, y que se halla a una distancia media de la costa de 9,5 km. Aquí destacan algunas zonas rocosas aisladas, varias zonas con gorgonias (*Eunicella singularis* (Esper) y *Leptogorgia sarmentosa* (Esper)), en las que abunda el bivalvo *Pteria hirundo* (Linnaeus, 1758). También es importante en esta zona una amplia extensión de concreciones calcáreas y coralinas situadas una entre Sitges y Vilanova, y otra frente a Vallcarca, formadas por típicos fondos de maërl, en los que abundan las algas calcáreas *Lithothamnion calcareum* (Pallas) Areschoug y *Lithothamniom corallioides* Crouan, principalmente.

"La Mar de Fora" es más variada y generalmente escarpada. Su profundidad va desde los 105 hasta los 1600 m en el canal de Foix. Destacan entre el S y SO de Vilanova una zona de barrancos submarinos que convergen hacia una profundidad de unos 500 m, un caladero muy rico en el centro, y unas planicies en cuyos límites, frente a Vallcarca, se encuentran los fondos de "El Parrusset". Éste es un cañón submarino profundo (los pescadores faenan a profundidades entre 200 y 450 m), de fondo rico en nódulos de ferromanganeso y que alberga una biocenosis de coral blanco (sensu PÉRÈS Y PICARD, 1964), asociada a una tanatocenosis de fauna Würmiense de gran interés malacológico.

MATERIAL Y MÉTODOS

El presente trabajo está basado en el material recolectado por los autores o proporcionado por pescadores durante más de una década. También se ha revisado material de colecciones malacológicas privadas de la zona de estudio.

El material ha sido recolectado en fondos arenosos, escolleras, rocas o acantilados mediante inmersión, y simultaneando con visitas a las diferentes playas de la zona, especialmente después de los temporales. Hay que tener en cuenta que las especies de aguas profundas que aparecen ocasionalmente en las playas o en aguas someras, suelen proceder de los restos arrojados al mar por los barcos pesqueros, o de la limpieza de las redes de pesca antes de entrar en el puerto.

La zona de la desembocadura del río Foix en Cubelles se ha muestreado quincenalmente durante más de un año (junio de 1992 a agosto de 1993) de una forma exhaustiva, volteando todas las piedras en dos transectos, uno de 15 x 1 m paralelo a la línea de costa y a 0,5 m de profundidad, y otro de 25 x 1 m, perpendicular a la costa y a una profundidad comprendida entre 0 y 1 m.

El material de aguas profundas ha sido proporcionado por pescadores de arrastre. Además, en más de 20 ocasiones durante el período de muestreo, se ha acompañado a los pescadores con objeto de separar el material por hábitats y profundidades *in situ*, para obtener una información más detallada sobre el mismo.

Se ha analizado el contenido estomacal de unos 3000 ejemplares de los asteroideos *Astropecten aranciacus* (L.) y *Astropecten irregularis* (Linck), procedentes de más de 50 arrastres, principalmente de fondos fangosos entre 40 y 350 m de profundidad. Se han estudiado también seis muestras de detrito fangoso (aproximadamente 20 kg en total) procedente de "El Parrusset", entre 200 y 350 m de profundidad, recolectadas entre 1994 y 1996. El detrito ha sido lavado y pasado por una serie de tamices, siendo el más fino de 0,4 mm de luz de malla. Además se han analizado unos 30 kg de sedimentos obtenidos en playas de la zona; unos 5 kg de sedimentos arenoso de 2 m de profundidad obtenidos en Sitges; y 1 kg de sedimento arenoso de 2 m de profundidad obtenido en el interior del puerto de Vallcarca. Una gran cantidad de micromoluscos se ha obtenido del estudio de estos sedimentos, lo que permite obtener un elevado número de especies, aunque de la mayor parte de

ellas se hallen sólo conchas (tanatocenosis), por lo que no es posible precisar sus hábitats.

La mayor parte del trabajo de Opistobranquios se ha basado en las publicaciones de BALLESTEROS (1977, 1978 y 1984), ROS (1975) y ASENSI (1984), y siempre que el material no haya sido recolectado por los autores, se indica la cita bibliográfica de la cual proviene.

Además, se han revisado las colecciones de A. Tubau, M. Roca y P. Ortoll, malacólogos aficionados o pescadores de Vilanova i la Geltrú. No ha sido posible, sin embargo localizar la colección de SAMÀ (1916), compuesta por 400 especies de moluscos procedentes del litoral entre Vilanova i la Geltrú (Barcelona) y Calafell (Tarragona).

El material fotografiado al microscopio electrónico de barrido (M.E.B.), ha sido previamente hervido en agua destilada y tratado con ultrasonidos, con el objeto de eliminar las impurezas depositadas en las conchas, aunque en algunos casos, cuando las conchas eran demasiado finas, no se ha realizado el tratamiento con ultrasonidos. Las muestras han sido fotografiadas en un MEB Hitachi S-2300 a 15KV. En algunos casos se han seleccionado para fotografiar ejemplares procedentes de otras zonas, con el objeto de ilustrar los ejemplares mejor conservados.

El listado de especies ha sido confeccionado siguiendo a SABELLI, GIANUZZI-SAVELLI Y BEDULLI (1990), excepto para algunos taxones, para los que se han empleado revisiones taxonómicas más recientes.

Parte del material aquí tratado ha sido cedido al Museu del Mar de Vilanova i la Geltrú.

RESULTADOS

El número total de especies de moluscos marinos recogidos en este trabajo es de 622 (7 Poliplacóforos, 417 Gasterópodos, 190 Bivalvos y 8 Escafópodos), correspondiendo aproximadamente un 2,7% a especies que se han encontrado exclusivamente en forma subfósil en el Garraf, algunas de las cuales no viven actualmente en el Mediterráneo, o habitan en zonas más profundas.

Lista de especies (Tabla I): A la izquierda aparece el nombre de cada especie, que irá en **negrita** en el caso de que sea objeto de comentarios en la discusión, irá precedida de un asterisco (*) cuando constituya primera cita en el Mediterráneo español, y de dos (**) cuando constituya primera cita en el Mediterráneo en general. A continuación se describe brevemente el tipo de hábitat donde se ha encontrado la especie (lo cual algunas veces no refleja su hábitat real) y el rango batimétrico: "s" (supralitoral), "m" (mesolitoral), "i" (infralitoral: de 0 a 30 m), "c" (circalitoral: de 30 a 200 m), y "b" (batial: más de 200 m). En algunos casos no se disponía de estos datos, por lo que no se registran. En el caso de las especies fósiles, tampoco se indica el hábitat. En la siguiente columna se señalan, con un número, las especies ilustradas, indicando dicho número el de la figura correspondiente. A continuación se señala la abundancia (+: 1-2 ejemplares, ++: 3-10, +++: 11-100, ++++: más de 100), y se identifican con una "p" a las especies procedentes del detrito de "El Parrusset" y con una "f" a aquellas que han sido halladas fósiles. En el caso de que las letras "p" y "f" aparezcan entre paréntesis, significa que la especie en cuestión no ha sido hallada exclusivamente en "El Parrusset" o no ha sido encontrada exclusivamente fósil, respectivamente. También se indica con una "v" si la especie ha sido hallada viva en el área de estudio, y con "Aa" o "Ai" se señalan las especies obtenidas en contenidos estomacales de *Astropecten aranciacus* o *A. irregularis*, respectivamente. Evidentemente no ha sido posible especificar todos los ambientes donde se han recolectado las muestras, y es por esto que nos hemos limitado a mencionar la procedencia de aquellas muestras obtenidas de estas formas particulares.

Tabla I. Listado de especies encontradas en el área de estudio, hábitat donde se han encontrado, rango batimétrico, figuras en las que están representadas, abundancia y procedencia.
Las especies en negrita están comentadas en el texto. No se incluyen los datos no disponibles de barimetría, ni de hábitat en las especies fósiles. En las especies de opistobranquios que no han sido recolectadas por los autores se incluye la referencia bibliográfica de donde procede la cita.
Códigos. *: primera cita en el Mediterráneo español; **: primera cita en el Mediterráneo; s: supralitoral; m: mesolitoral; i infralitoral (0-30 m); c: circalitoral (30-200 m); b: batial (>200 m); +: 1-2 ejemplares; ++: 3-10 ejemplares; +++: 11-100 ejemplares; ++++: más de 100 ejemplares; p: especie procedente del detrito de El Parrusset; f: especies halladas fósiles; (p): especie hallada no sólo en El Parrusset; (f): especie hallada no exclusivamente fósil; v: especie encontrada viva en el área de estudio; Aa: especie obtenida en contenido estomacal de *Astropecten aranciacus*; Ai: *idem* de *Astropecten irregularis*.
Table I. List of species found in the study area, habitat where they have been collected, bathymetric range, figures when included, abundance and other data related with their collection.
Species in bold are discussed in the text. Data on bathymetric range are included only when known, habitat of fossil species always excluded. A bibliographic reference is given for the opisthobranch species not collected by the authors.
*Codes. *: first record in the Spanish Mediterranean; **: first record in the Mediterranean Sea; s: upper littoral; m: midlittoral; i lower littoral (0-30 m); c: circa littoral (30-200 m); b: bathyal (>200 m); +: 1-2 specimens; ++: 3-10 specimens; +++: 11-100 specimens; ++++: more than 100 specimens; p: species found in El Parrusset detritus; f: species found fossil; (p): species found not only in El Parrusset; (f): species found not only fossil; v: species found alive in the study area; Aa: species collected in* Astropecten aranciacus *gut contents; Ai: idem in* Astropecten irregularis *gut contents.*

Clase POLYPLACOPHORA			
Familia LEPTOCHITONIDAE			
Lepidopleurus cajetanus (Poli, 1791): piedras, i		+	v
Familia ISCHNOCHITONIDAE			
Callochiton septemvalvis euplaeae (O. G. Costa, 1829): algas (*Payssonnelia*) y conchas muertas, i-c		++	v
Lepidochitona cinerea (Linnaeus, 1767): piedras y espigones, m-i		+++	v
Lepidochitona corrugata (Reeve, 1848): piedras y espigones, m-i		+++	v
Familia CHITONIDAE			
Chiton olivaceus Spengler, 1797: piedras y espigones, m-i		+++	v
Familia ACANTHOCHITONIDAE			
Acanthochitona crinita (Pennant, 1777): piedras, i		+++	v, Aa
Acanthochitona fascicularis (Linnaeus, 1767): piedras y conchas muertas, i-c		++	v
Clase GASTROPODA			
Familia PATELLIDAE			
Patella caerulea Linnaeus, 1758: rocas y espigones, m-i		++++	v
Patella rustica Linnaeus, 1758: rocas y espigones, s-i		++++	v
Patella ulyssiponensis Gmelin, 1791: rocas y espigones, i		+++	v
Familia ACMAEIDAE			
Acmaea virginea (O. F. Müller, 1776): sedimentos en zonas rocosas, i		++	
Familia LEPETIDAE			
***Iothia fulva* (O. F. Müller, 1776)**: b		+	p, f
Familia COCCULINIDAE			
Coccopigya sp.: b		+	p
Familia LEPETELLIDAE			
***Lepetella* cfr. *espinosae* Dantart y Luque, 1994**: b		+++	p
Familia ADDISONIIDAE			
***Addisonia excentrica* Tiberi, 1857**: en capsula ovígeras de *Scyliorrhinus*, c-a	Fig. 3	++	(p), v
Familia NERITIDAE			
Smaragdia viridis (Linnaeus, 1758): fango, i-c		++	Aa

Familia FISSURELLIDAE			
Fissurella nubecula (Linnaeus, 1758): en rocas y piedras, m-i		+++	v
Diodora gibberula (Lamarck, 1822): en piedras, i		++	v
Diodora graeca (Linnaeus, 1758): en rocas y piedras, i		+++	v
Emarginula fissura (Linnaeus, 1758): b		++	(p), v
Emarginula octaviana Coen, 1939: i-c		+++	
****Emarginula pustula*** **Thiele in Kuester, 1913**: b	Fig. 4	+	p
Emarginula rosea T. Bell, 1824: c-b		++	(p), v
Familia SCISSURELLIDAE			
Anatoma aspera **(Philippi, 1844)**: b		+++	p
Familia HALIOTIDAE			
Haliotis tuberculata lamellosa Lamarck, 1822: i		++	
Familia TROCHIDAE			
Clanculus cruciatus (Linnaeus, 1758): piedras, i		++	v
Clanculus jussieui (Payraudeau, 1826): piedras, i		++	v
Jujubinus exasperatus (Pennant, 1777): i-c		+++	Aa
Jujubinus montagui (W. Wood, 1828): fango, c		+++	v, Aa
Jujubinus striatus (Linnaeus, 1758): fango, c		++	v, Aa
Gibbula albida (Gmelin, 1791)		+	
Gibbula magus (Linnaeus, 1758): cascajo y mäerl, c		++++	v, Aa
Gibbula racketti (Payraudeau, 1826): piedras, i		++++	v
Gibbula fanulum (Gmelin, 1791)		++	
Gibbula guttadauri (Philippi, 1836)		+	
Gibbula leucophaea (Philippi, 1836)		++	
Gibbula philberti (Récluz, 1843): piedras y espigones, m		++++	v
Gibbula richardi (Payraudeau, 1826): piedras, m		+++	v
Gibbula varia (Linnaeus, 1758): piedras, m		+++	v
Gibbula divaricata (Linnaeus, 1758): piedras, m		++++	v
Osilinus articulatus Lamarck, 1822: piedras, m		++	v
Osilinus turbinatus (Born, 1778): piedras, m		++	v
Calliostoma conulus (Linnaeus, 1758): rocas y mäers, i-c		+++	v, Aa
Calliostoma dubium (Philippi, 1844)		+	
Calliostoma laugieri laugieri (Payraudeau, 1826): i		++	
Calliostoma zizyphinum (Linnaeus, 1758)		+	(p), f
Calliostoma granulatum (Born, 1778): fango, c-b		+++	v, Aa
Danilia otaviana (Cantraine, 1835): b	Fig. 5	++	p, (f)
Familia SKENEIDAE			
Dikoleps pusilla (Jeffreys, 1847): b		+	p
**Lissotesta gittenbergeri* (van Aartsen y Bogi, 1988): b		+	p
Familia TURBINIDAE			
Bolma rugosa (Linnaeus, 1767): rocas y fango, c-b		+++	v
Familia COLLONIIDAE			
Homalopoma sanguineum (Linnaeus, 1758)		+	
Familia TRICOLIIDAE			
Tricolia pullus (Linnaeus, 1758): i		++++	
Tricolia speciosa (von Mühlfeldt, 1824): i		++	
Tricolia tenuis (Michaud, 1829): i		++	
Familia CERITHIIDAE			
Cerithium alucaster (Brocchi, 1814): fango y mäerl, i-c		+++	v, Aa
Cerithium lividulum Risso, 1826		+	
Cerithium vulgatum Bruguière, 1792: fango y mäerl, i-c		+++	v
Bittium latreillei (Payraudeau, 1826): i-c		+++	v, Aa
Bittium reticulatum (da Costa, 1778): b		++	(p), v, Ai
Bittium submamillatum (Rayneval y Ponzi, 1854): fango y fondos detríticos, c		++	(p), (f), Ai

Familia FOSSARIDAE			
Fossarus ambiguus (Linnaeus, 1758): i		+++	
Familia SILIQUARIIDAE			
Tenagodus obtusus (Schumacher, 1817)		+	p, f
Familia TURRITELLIDAE			
Turritella communis Risso, 1826: fango, c		++++	v, Aa
Turritella monterosatoi Kobelt, 1888: fango, c		+++	(p), (f), v, Aa
Familia LITTORINIDAE			
Littorina neritoides (Linnaeus, 1758): rocas y espigones, s		++++	v
Littorina punctata (Gmelin, 1791): rocas y espigones, s		++++	v
Familia SKENEOPSIDAE			
Skeneopsis planorbis (Fabricius, 1780): arena, i		++++	v
Familia RISSOIDAE			
Rissoa auriscalpium (Linnaeus, 1758): i		+++	
Rissoa decorata Philippi, 1846: i		+++	
****Rissoa gemmula*** **(Fischer in de Folin, 1871)**: i	Figs. 2, 20-21	+	
Rissoa guerinii Récluz, 1843: i		+++	
Rissoa labiosa (Montagu, 1803): i		++	
Rissoa lia (Monterosato, 1884 ex Benoit ms.): i		++	
Rissoa monodonta Philippi, 1836: i		+++	
Rissoa similis Scacchi, 1836: i		++++	
Rissoa ventricosa Desmarest, 1814: i		+++	
Rissoa violacea Desmarest, 1814: i		+++	
Alvania beani (Hanley in Thorpe, 1844): i		++	Ai
Alvania cancellata (da Costa, 1778): i		+++	
Alvania cimex (Linnaeus, 1758): i		+++	
Alvania cimicoides **(Forbes, 1844)**: fango y detrito coralígeno, c-b		+++	(p), v, Ai
Alvania discors (Allan, 1818): i		++	
Alvania geryonia (Nardo, 1847 ex Chiereghini ms.): i		++	
Alvania lactea (Michaud, 1832): i		+++	
Alvania lineata Risso, 1826: i		+++	
Alvania punctura (Montagu, 1803): fango y detrito coralígeno, c-b		+++	(p), v, Ai
Alvania rudis (Philippi, 1844): i		++	
Alvania subcrenulata (B. D. D., 1884): i		+++	
**Alvania subsoluta* (Aradas, 1847): b	Figs. 8, 11, 12	++	p, f
Alvania testae **(Aradas y Maggiore, 1844)**: fango y detrito coralígeno, c-b	Figs. 7, 9, 10	++++	(p), v, Ai
****Alvania zylensis*** **Gofas y Warén, 1982**: b	Figs. 13, 14	+	p
Alvania semistriata (Montagu, 1808): i-b		+++	(p)
Alvania carinata (da Costa, 1778): i		++	
**Benthonella tenella* (Jeffreys, 1869): fango, c		++	Ai
Manzonia crassa (Kanmacher, 1798): i		+++	
Manzonia zetlandica (Montagu, 1815): b		++	p
Obtusella intersecta (S. W. Wood, 1857): b		+	p
Obtusella macilenta **(Monterosato, 1880)**: fango y detrito coralígeno, c-b	Fig. 6	++++	(p), v, Ai
Pusillina inconspicua (Alder, 1844): i-b	Figs. 17, 18, 19	+++	(p), Ai
Pusillina philippi (Aradas y Maggiore, 1844): i-b	Figs. 15, 16	+++	(p), (f), Ai
Pusillina radiata (Philippi, 1836): i		++	
Setia maculata (Monterosato, 1869): i		++	
Rissoina bruguierei (Payraudeau, 1826): i		+++	
Familia ADEORBIDAE			
Circulus striatus (Philippi, 1836): i		++	
Familia ASSIMINEIDAE			
Paludinella sicana (Brugnone, 1876): i		+++	

Familia CAECIDAE			
Caecum auriculatum de Folin, 1868: i		++	
Caecum clarkii Carpenter, 1858: i		++	
Caecum trachea (Montagu, 1803): i		++	
Familia HYDROBIIDAE			
Ventrosia ventrosa (Montagu, 1803)		++	
Familia IRAVADIIDAE			
Ceratia proxima (Forbes y Hanley, 1850 ex Alder ms.): fango y detrito coralígeno, c-b		+++	(p), v, Ai
Hyala vitrea (Montagu, 1803): fango y detrito coralígeno, c-b		++	(p), v, Ai
Familia TORNIDAE			
Tornus subcarinatus (Montagu, 1803): i		+++	
Familia TRUNCATELLIDAE			
Truncatella subcylindrica (Linnaeus, 1767): i		+++	
Familia APORRHAIDAE			
Aporrhais pespelecani (Linnaeus, 1758): fango, c		++++	v, Ai
Aporrhais serresianus (Michaud, 1828): fango, c-b		+++	(p), v
Familia VANIKORIDAE			
**Talassia dagueneti* (de Folin, 1873): b	Fig. 31	+	p
Familia CALYPTRAEIDAE			
Calyptraea chinensis (Linnaeus, 1758): en conchas muertas, c-b		++++	(p), v
***Crepidula fornicata* (Linnaeus, 1758)**		+	
Crepidula unguiformis Lamarck, 1822: en conchas muertas, c-b		+++	v
Familia CAPULIDAE			
Capulus ungaricus (Linnaeus, 1758): sobre conchas, c-b		+++	(p), (f), v
Familia XENOPHORIDAE			
Xenophora crispa (Koenig, 1825): fango y fondos detríticos, b		+++	(p), v
Familia VERMETIDAE			
Vermetus triquetrus Bivona, 1832: rocas, i		+++	v
Serpulorbis arenaria (Linnaeus, 1767): rocas, i		+++	v
Familia CYPRAEIDAE			
Erosaria spurca (Linnaeus, 1758)		+	
Luria lurida (Linnaeus, 1758)		+	
Zonaria pyrum (Gmelin, 1791): mäerl, c		+++	v
Familia OVULIDAE			
Aperiovula adriatica (G. B. Sowerby I, 1828): c		++	v
Neosimnia spelta (Linnaeus, 1758): sobre *Eunicella*, c		++	v
Pseudosimnia carnea (Poiret, 1789): c		++	v
Familia LAMELLARIIDAE			
Lamellaria latens (O. F. Müller, 1776): i		+	
Familia TRIVIIDAE			
Trivia arctica (Pulteney, 1789): i		++	
Trivia monacha (da Costa, 1778): i		+++	
Trivia multilirata (G. B. Sowerby II, 1870)		++	p, f
Erato voluta (Montagu, 1803)		+	f
Familia NATICIDAE			
Naticarius cruentatus (Martyn, 1784): arena y fango, i-c		++++	v
Naticarius dillwyni (Payraudeau, 1826): arena, i		++	
Naticarius punctatus (Chemnitz in Karsten, 1789)		+	
Naticarius vittatus (Gmelin, 1791)		+	
Tectonatica filosa (Philippi, 1844): fango, c		+++	v, Aa
Lunatia fusca (Blainville, 1825): fango, c-b		++++	(p), v, Aa
Lunatia guillemini (Payraudeau, 1826): fango, i-c		++	
Lunatia macilenta (Philippi, 1844): arena y fango, i-c		+++	v, Aa
Lunatia nitida (Donovan, 1804): arena y fango, i-c		+++	v, Aa
Payraudeautia intricata (Donovan, 1804): fango y mäerl, i-c		+++	Aa

Familia TONNIDAE			
Tonna galea (Linnaeus, 1758)		+	
Familia CASSIDAE			
Galeodea echinophora (Linnaeus, 1758): fango, c		+++	v
Galeodea rugosa (Linnaeus, 1771): fango, c-b		++	(p), v
Phalium granulatum (Born, 1778): fango, c		+++	v
Phalium saburon (Bruguière, 1792): fango, c		++	v
Familia RANELLIDAE			
Ranella olearia (Linnaeus, 1758)		+	p, f
Cymatium corrugatum (Lamarck, 1816): fango, c		++++	v
Cymatium parthenopeum parthenopeum (von Salis, 1793): rocas, i		+	v
Cabestana cutacea cutacea (Linnaeus, 1767): fango y rocas, i-c		++	v
Charonia lampas lampas (Linnaeus, 1758)		+	
Familia ATLANTIDAE			
Atlanta peronii Lesueur, 1817: fango y detrito coralígeno, b		++	(p), Ai
Oxygyrus keraudrenii (Lesueur, 1817): b		++	p
Familia TRIPHORIDAE			
Marshallora adversa (Montagu, 1803): fondos detríticos, i		+++	v, Ai
Monophorus erythrosomus (Bouchet y Guillemot, 1978): i		++	
Monophorus perversus (Linnaeus, 1758): i		+++	
**Obesula marinostri* Bouchet, 1985: b		+	p
Similiphora similior (Bouchet y Guillemot, 1978): i		++	
Metaxia metaxae (delle Chiaje, 1828): i-b		++	(p), (f)
Familia CERITHIOPSIDAE			
**Cerithiopsis diadema* Monterosato, 1874 ex Watson ms.: b	Fig. 22	+	p
Cerithiopsis jeffreysi Watson, 1885: b	Fig. 23	++	(p), (f)
Cerithiopsis minima (Brusina, 1865): i	Fig. 24	+++	
Cerithiopsis nana Jeffreys, 1867: i-b	Figs. 25, 29	++	(p), (f)
Cerithiopsis scalaris (Monterosato, 1877): b	Fig. 26	+++	(p), (f)
**Cerithiopsis tiara* Monterosato, 1874 ex Watson ms.: b	Fig. 27	+	(p), (f)
Cerithiopsis tubercularis (Montagu, 1803): i-b	Figs. 28, 30	+++	(p), (f)
Familia ACLIDIDAE			
**Aclis attenuans* Jeffreys, 1883: fango y detrito coralígeno, b		+++	(p), v, Ai
Aclis gulsonae (W. Clark, 1850): fango y detrito coralígeno, b		+	p, v, Ai
Cima minima (Jeffreys, 1858): b		++	(p)
**Cioniscus gracilis* Monterosato, 1874, ex Jeffreys ms.: b		++	(p)
Graphis albida (Kanmacher, 1798): i-b	Figs. 32, 33, 34	++	(p)
Familia EPITONIIDAE			
**Epitonium aculeatum* (Allan, 1818): fango y detrito coralígeno, b		++	(p), v, Ai
Epitonium algerianum (Weinkauff, 1866): b		++	(p)
**Epitonium celesti* (Aradas, 1854): b		+	p
Epitonium clathratulum (Kanmacher, 1798): b	Fig. 39	++	(p)
Epitonium commune (Lamarck, 1822): rocas y fango, i-c		+++	v, Aa
**Epitonium dendrophylliae* Bouchet y Warén, 1986: b		+	p
**Epitonium hispidulum* (Monterosato, 1874): b		++	(p)
**Epitonium linctum* (de Boury y Monterosato, 1890): b	Fig. 40	+	p
Epitonium pulchellum (Bivona, 1832): i		++	
Epitonium turtonis (Turton, 1819): fango, c		+++	v, Aa
Cirsotrema cochlea (G. B. Sowerby II, 1844): i		+	
Gyroscala lamellosa (Lamarck, 1822): rocas y arena, i		+++	v
**Opalia abboti* Clench y Turner, 1952: b		++	p
Opalia crenata (Linnaeus, 1758): i		++	
Opalia hellenica (Forbes, 1844): b		+	p

Familia EULIMIDAE			
Eulima bilineata Alder, 1848: fango y detrito coralígeno, b		++	(p), v, Ai
Eulima glabra (da Costa, 1778): i		+++	
****Crinophtheiros* sp.:** fango, b	Figs. 37, 38	++	Ai
**Entoconcha mirabilis* Müller, 1852: b		+	p
Melanella alba (da Costa, 1778): i		++	
Melanella boscii (Payraudeau, 1827): i		+++	
Melanella praecurta (Pallary, 1904): fango, b		++	
***Parvioris ibizenca* (Nordsieck, 1968)**: i		++	
Sticteulima jeffreysiana (Brusina, 1869): detrito coralígeno, b		+	p, v
Vitreolina perminima (Jeffreys, 1883): detrito coralígeno, b	Figs. 35, 36	+++	(p), v
***Vitreolina* sp.:** detrito coralígeno, b		++	(p), Ai
Familia MURICIDAE			
Bolinus brandaris (Linnaeus, 1758): fango, arena y piedras, i		++++	v
Hadriania craticuloides (Vokes, 1964): fango y detrito coralígeno, c-b		++	(p), v, Aa
Hexaplex trunculus (Linnaeus, 1758): fango, rocas y espigones, i		++++	v
Murexul aradasii (Poirier, 1883 ex Monterosato ms.)		+	p, f
Muricopsis cristatus (Brocchi, 1814): rocas y detritos, i-c		++	v
Ocenebra erinaceus (Linnaeus, 1758): rocas y detritos, i-c		+++	v
Ocinebrina aciculata (Lamarck, 1822): fango y piedras, i-c		++	v, Aa
Ocinebrina edwardsi (Payraudeau, 1826): rocas y piedras, i		++++	v
****Trophon barvicensis* (Johnston, 1825)**	Fig. 45	+	p, f
***Trophon echinatus* (Kiener, 1840)**: b	Figs. 41, 42	++	p
***Trophon* sp.:** b	Figs. 43, 44	++	p
Trophon muricatus (Montagu, 1803): fango y detrito coralígeno, b	Figs. 46, 47	+++	(p), v, Ai
Familia BUCCINIDAE			
Buccinum humphreysianum Bennet, 1824: b		++	v
Buccinum undatum Linnaeus, 1758: fango, c		++	(p), f
Buccinulum corneum (Linnaeus, 1758): fango y rocas, i-c		+++	v
Chauvetia brunnea (Donovan, 1804): i		++	
Chauvetia turritellata (Deshayes, 1835): i		++	
Colus jeffreysianus (Fischer, 1868): i		+	
Neptunea contraria (Linnaeus, 1771)		++	(p), f
Pisania striata (Gmelin, 1791)		+	
Cantharus dorbignyi (Payraudeau, 1826): i		+	
Familia CORALLIOPHILIDAE			
Coralliophila meyendorffi (Calcara, 1845): piedras y fango, i		++	v
Coralliophila panormitana (Monterosato, 1869): b		+	p
Coralliophila squamosa (Bivona, 1831): fango, c-b		+++	(p), v
Familia FASCIOLARIIDAE			
Fusinus pulchellus (Philippi, 1844): fango, i		+++	v, Aa
Fusinus rostratus (Olivi, 1792): fango, c		+++	(p), v
Fusinus rudis (Linnaeus, 1758): fango, i		++	Aa
Familia NASSARIIDAE			
Nassarius corniculus (Olivi, 1792): piedras, i		++	v
Nassarius cuvierii (Payraudeau, 1826): arena, i		++++	v
Nassarius incrassatus (Ström, 1768): piedras, i		++++	v, Aa
Nassarius mutabilis (Linnaeus, 1758): arena y fango, i		++++	v, Aa
Nassarius nitidus (Jeffreys, 1867): i		++	v
Nassarius pygmaeus (Lamarck, 1822): fango y piedras, i-c		++++	v, Aa
Nassarius reticulatus (Linnaeus, 1758): arena, i		++++	v, Aa
Nassarius unifasciatus (Kiener, 1835)		++	
Naytiopsis granum (Lamarck, 1822): arena, i		+++	v
Cyclope neritea (Linnaeus, 1758)		+	

Familia THAIDIDAE			
Orania fusulus (Brocchi, 1814)		+	
Stramonita haemastoma (Linnaeus, 1766): rocas, i		++++	v
Familia COLUMBELLIDAE			
Columbella rustica (Linnaeus, 1758): rocas y algas, i		++	v
Mitrella minor (Scacchi, 1836)		+	p, f
Mitrella scripta (Linnaeus, 1758)		+	
Familia COSTELLARIIDAE			
Vexillum ebenus (Lamarck, 1811): i		++	
Vexillum tricolor (Gmelin, 1790)		+	
Familia MARGINELLIDAE			
Gibberula caelata (Monterosato, 1877)		++	
Gibberula miliaria (Linnaeus, 1758): arena, i		++++	
Gibberula philippii (Monterosato, 1877): i		+++	
Gibberula turgidula (Locard y Caziot, 1900): fango, c		++	(p), Ai
Volvarina mitrella (Risso, 1826)		+	
Granulina clandestina (Brocchi, 1814): b		+	p
Familia MITRIDAE			
Mitra zonata Marryat, 1818: fango y mäerl, i-c		++	v
Familia CANCELLARIIDAE			
Cancellaria cancellata (Linnaeus, 1767): arena y fango, i-c		++++	v
Cancellaria similis Sowerby, 1833: fango, c-b		++	v
Familia CONIDAE			
Conus ventricosus (Gmelin, 1791): i		++	
Familia TURRIDAE			
Bela brachistoma (Philippi, 1844): fango y detrito coralígeno, c-b	Figs. 48, 49	++++	(p), v, Ai
Bela laevigata (Philippi, 1836): arena, i		+++	v
Bela menkhorsti van Aartsen, 1988: b		+	p
Bela nebula (Montagu, 1803): arena fangosa, i		+++	Ai
Bela ornata (Locard, 1897): fango, i-c		++	Aa
Bela zonata (Locard, 1892): fango, c		++	Ai
***Mangelia attenuata* (Montagu, 1803)**: fango y detrito coralígeno, i-b	Figs. 50, 51	+++	(p), v, Aa, Ai
***Mangelia costata* (Donovan, 1804)**: fango y detrito coralígeno, c-b		++	(p), v, Ai
Mangelia cfr. *goodalii* Reeve, 1846: i		++	
***Mangelia nuperrima* (Tiberi, 1855)**: fango y detrito coralígeno, c-b	Figs. 52, 53	++	(p), Ai
Mangelia paciniana (Calcara, 1839): arena, i		++	
***Mangelia serga* (Dall, 1881)**: fango y detrito coralígeno, c-b	Figs. 54, 55	++	(p), v, Ai
Mangelia smithi (Forbes, 1844): arena, fango y detrito coralígeno, c-b		++	(p), Ai
Mangelia stossiciana (Brusina, 1869): i		+++	
Mangelia unifasciata Deshayes, 1835: arena y fango, i		+++	v, Ai
Mangelia vauquelini (Payraudeau, 1826): arena, i		++	
Mangiliella bertrandii (Payraudeau, 1826): i		+	
Mangiliella taeniata (Deshayes, 1835): i		++	
***Taranis moerchi* (Malm, 1861)**: detrito coralígeno, b	Figs. 57, 58, 59	+++	p
***Taranis* sp.**: detrito coralígeno, b	Figs. 60, 61, 62	+	p
***Microdrilia loprestiana* (Calcara, 1841)**: fango y detrito coralígeno, c-b	Fig. 56	+++	v, Ai
Haedropleura septangularis (Montagu, 1803): en *Posidonia*, i		+++	
*******Pleurotomella coeloraphe*** (Dautzenberg y Fischer, 1896)**: b	Figs. 63, 64, 65	++	p
******Pleurotomella demosia*** (Dautzenberg y Fischer, 1896)**: b	Figs. 66, 67, 68	++	(p), v, Ai
Crassopleura maravignae Bivona, 1838: i-c		++	Aa
Mitrolumna olivoidea (Cantraine, 1835): i		++	(p), (f)
Raphitoma aequalis Jeffreys, 1867: fango, c		++	Aa
Raphitoma bicolor (Risso, 1826): arena, i		++	
Raphitoma concinna (Scacchi, 1836): arena, i		++	

**Raphitoma cordieri* (Payraudeau, 1826): i		+	
Raphitoma echinata (Brocchi, 1814): i		+	
Raphitoma horrida Monterosato, 1844: en *Posidonia*, i		++	
Raphitoma leufroyi (Michaud, 1828): arena, i		++	
Raphitoma linearis (Montagu, 1803): arena, i		+++	
Raphitoma cfr. nivea (Marshall in Sykes, 1906): i		+	
**Raphitoma pupoides* (Monterosato, 1884): i		++	
Comarmondia gracilis (Montagu, 1803): fango y arena, i-c		++	(p), v, Aa
Teretia teres (Forbes, 1844): fango y detrito coralígeno, b	Fig. 69	+++	(p), v, Ai
Familia TJAERNOEIDAE			
***Tjaernoeia exquisita* (Jeffreys, 1883): b**		+	p
Familia ARCHITECTONICIDAE			
***Basisulcata lepida* (Bayer, 1942)**: mäerl, c		+	v
Heliacus alleryi (Seguenza, 1876): b		++	p
Heliacus architae (O. G. Costa, 1867): b		++	p
Familia MATHILDIDAE			
Mathilda cochlaeformis Brugnone, 1873: b		+++	p
Familia OMALOGYRIDAE			
Omalogyra atomus (Philippi, 1841): i		+++	
Ammonicera fischeriana (Monterosato, 1869): i		+++	
Familia PYRAMIDELLIDAE			
Tiberia minuscula (Monterosato, 1880): fango y detrito coralígeno, c-		+	p, v, Ai
Chrysallida brattstroemi Warén, 1991: b	Fig. 70	+++	p
Chrysallida brusinai (Cossmann, 1921): i		++++	
***Chrysallida dollfusi* (Kobelt, 1903)**: b	Fig. 71	+	p
Chrysallida emaciata (Brusina, 1866): i		++	
Chrysallida excavata (Philippi, 1836): i		+++	
Chrysallida fenestrata (Jrffreys, 1848): c		++	Ai
Chrysallida flexuosa (Monterosato, 1874 ex Jeffreys): fango y detrito coralígeno, c-b		++	(p), v, Ai
Chrysallida ghisottii van Aartsen, 1984: i		++	
Chrysallida indistincta (Montagu, 1808): i		++	
Chrysallida intermixta (Monterosato, 1884)		++	
Chrysallida interstincta (J. Adams, 1797): i		++	
Chrysallida juliae (de Folin, 1872): fango, c		++	Ai
Chrysallida palazzii Micali, 1984: fango y detrito coralígeno, c-b		++	(p), v, Ai
***Chrysallida pellucida* (Dillwyn, 1817)**		+	p, f
Chrysallida suturalis (Philippi, 1844): fango y detrito coralígeno, c-b		+++	(p), v, Ai
Odostomella doliolum (Philippi, 1844): i-b		++	(p)
Euparthenia bulinea (Lowe, 1841): arena, i		++	
Euparthenia humboldti (Risso, 1826)		+	
Eulimella acicula (Philippi, 1836)		++	Ai
Eulimella ataktos Warén, 1991: fango y detrito coralígeno, c-b	Fig. 72	+++	(p), v, Ai
Eulimella bogii van Aartsen, 1994: b		++	p
Eulimella scillae (Scacchi, 1835): fango y detrito coralígeno, c-b		+++	(p), v, Ai
***Eulimella unifasciata* (Forbes, 1844)**: fango y detrito coralígeno,	Fig. 74	++	(p), v, Ai
***Eulimella ventricosa* (Forbes, 1844)**: fango y detrito coralígeno, c-b	Fig. 73	++	
Puposyrnola minuta (H. Adams, 1869): fango y detrito coralígeno, b		++	(p), v, Ai
Odostomia acuta Jeffreys, 1848: fango y arena, i-c		++	
Odostomia afzelii (Warén, 1991): fango y detrito coralígeno, c-b	Fig. 75	++	(p), v, Ai
Odostomia carrozzai van Aartsen, 1987: i		++	
Odostomia clavulus (Lovén, 1846): fango y detrito coralígeno, c-b		+++	(p), v
Odostomia conoidea (Brocchi, 1814): fango y detrito coralígeno, i-b		++++	(p), v, Ai
Odostomia erjaveciana Brusina, 1869: arena, i		++	
Odostomia eulimoides Hanley, 1844: i		+++	

Odostomia hansgei (Warén, 1991): fango y detrito coralígeno, b	Fig. 76	+++	(p), v
Odostomia kromi van Aartsen, Menkhorst y Gittenberger, 1984: i		++	
Odostomia lukisii Jeffreys, 1859: i		+++	
Odostomia megerlei (Locard, 1886)		++	
Odostomia plicata (Montagu, 1803): i		++++	
Odostomia scalaris MacGillivray, 1843: i		++	
Odostomia striolata Forbes y Hanley, 1850: i-b		+++	(p), (f)
Odostomia suboblonga Jeffreys, 1884: b		++	p
Odostomia turriculata Monterosato, 1869: i		+	
Odostomia turrita Hanley, 1844: i-b		+++	(p)
Odostomia umbilicaris Malm, 1863: fango y detrito coralígeno, c-b		++++	(p), v, Ai
Odostomia unidentata (Montagu, 1803): fango y detrito coralígeno, i-b		++	(p), Ai
Odostomia verduini van Aartsen, 1987: i		++	
Noemiamea dolioliformis (Jeffreys, 1848): i		++	
Ondina dilucida (Monterosato, 1844): fango, c		+	Ai
Ondina obliqua (Alder, 1844): i		++	
Turbonilla acuta (Donovan, 1804): i		++	
***Turbonilla acutissima* Monterosato, 1884**: b	Fig. 77	++	p
Turbonilla jeffreysii (Jeffreys, 1848): i		+++	
Turbonilla pusilla (Philippi, 1844)		+	
Turbonilla rufa (Philippi, 1836): i		++	(p), (f)
Turbonilla sinuosa (Jeffreys, 1884): i		++	
Turbonilla striatula (Linnaeus, 1758)		++	
Ebala nitidissima (Montagu, 1803)		++	
Ebala pointeli (de Folin, 1868): i		++	
Ebala sp.: b		+	p
Familia ACTEONIDAE			
Acteon tornatilis (Linnaeus, 1758): arena y fango, i-c		++	Ai
Crenilabrum exilis (Forbes in Jeffreys, 1870): i-b		++	(p)
Familia DIAPHANIDAE			
Diaphana minuta Brown, 1827: b		++	(p), Ai
Familia RETUSIDAE			
Retusa semisulcata (Philippi, 1836): i		+++	
Retusa truncatula (Bruguière, 1792): i		+++	
Cylichnina umbilicata (Montagu, 1803): fango, i-c		+++	Ai
Familia RINGICULIDAE			
Ringicula auriculata (Ménard de la Groye, 1811): fango, c	Figs. 80, 81	++	Ai
**Ringicula* cfr. *leptocheila* Brugnone, 1873: b	Figs. 78, 79	+	p
Familia BULLIDAE			
Bulla striata Bruguière, 1792: arena, i		++++	
Familia HAMINAEIDAE			
Haminaea hydatis (Linnaeus, 1758): i		++	
Haminaea orbignyana (Férussac, 1822): i		++	
Weinkauffia turgidula (Forbes, 1844): b		++	(p), Ai
Familia PHILINIDAE			
Philine aperta (Linnaeus, 1767): i		++	
Philine catena (Montagu, 1803): i		++	
Philine scabra (O. F. Müller, 1776): i-b		++	(p)
**Laona pruinosa* (Clark, 1827): fango y detrito coralígeno, c-b		++	(p), Ai
Familia SCAPHANDRIDAE			
Cylichna cylindracea (Pennant, 1777): fango y detrito coralígeno, c-b	Fig. 82	+++	(p), Ai
Roxania utriculus (Brocchi, 1814): fango, c		++	Ai
Scaphander lignarius (Linnaeus, 1758): fango, c		+++	v
***Scaphander punctostriatus* (Mighels y Adams, 1841)**: b		++	p

Familia CAVOLINIIDAE				
Cavolinia inflexa (Lesueur, 1813)		+++	p	
Clio cuspidata (Bosc, 1802)		+++	p	
Clio pyramidata Linnaeus, 1767		+++	p	
Creseis acicula Rang, 1828		+++	p	
Styliola subula (Quoy y Gaimard, 1827)		+++	p	
Familia LIMACINIDAE				
**Limacina bulimoides* (d'Orbigny, 1836): b		++	p	
Limacina inflata (d'Orbigny, 1836): b		++	p	
**Limacina retroversa* (Fleming, 1822): b	Fig. 83	++++	p	
Familia PERACLIDAE				
Peracle reticulata (d'Orbigny, 1836): b	Figs. 84, 85	+	p	
Familia ELYSIIDAE				
Elysia viridis (Montagu, 1810)				Ballesteros (1984)
Familia HERMAEIDAE				
Stiliger sp.				Ballesteros (1984)
Familia UMBRACULIDAE				
Umbraculum mediterraneum (Lamarck, 1819): fango, c		+	v	
Familia APLYSIIDAE				
Aplysia depilans Gmelin, 1791				Ros (1975)
Aplysia fasciata Poiret, 1789: arena, i		++	v	
Aplysia punctata Cuvier, 1803: arena, i		++	v	
Familia TRITONIIDAE				
Tritonia hombergi Cuvier, 1803				Ros (1975)
Familia DOTIDAE				
Doto koenneckeri Lemche, 1976				Ballesteros (1984)
Familia TRIOPHIDAE				
Kaloplocamus ramosus (Cantraine, 1835)				Ros (1975)
Familia POLYCERIDAE				
Polycera quadrilineata (O. F. Müller, 1776): piedras, i		+	v	
Familia DORIDIDAE				
Doris verrucosa Linnaeus, 1758: detritos y piedras, i		++	v	
Familia ARCHIDORIDIDAE				
Archidoris tuberculata (Cuvier, 1804)				Ros (1975)
Familia DISCODORIDIDAE				
***Taringa faba* (Ballesteros, Llera y Ortea, 1984)**: bajo piedras, zona detrítica, i		++	v	
Familia CENTRODORIDIDAE				
Jorunna tomentosa (Cuvier, 1804)				Ballesteros (1984)
Familia DENDRODORIDIDAE				
Dendrodoris grandiflora (Rapp, 1827): bajo piedras, zona detrítica, i		++	v	
Doriopsilla areolata Bergh, 1880				Asensi (1984)
Familia ARMINIDAE				
Armina maculata Rafinesque, 1814				Ballesteros (1981)
Familia FLABELLINIDAE				
Calmella cavolini (Verany, 1846)				Ballesteros (1978)
Coryphella pedata (Montagu, 1822)				Ballesteros (1984)
Familia TERGIPEDIDAE				
Tergipes tergipes (Forskal, 1775)				Asensi (1984)
Familia EUBRANCHIDAE				
Eubranchus exiguus (Alder y Hancock, 1848)				Asensi (1984)
Eubranchus farrani (Alder y Hancock, 1844)				Ballesteros (1984)
Familia FACELINIDAE				
Cratena peregrina Gmelin, 1791				Ballesteros (1978)
Facelina coronata (Forbes y Goodsir, 1839)				Ballesteros (1984)
Facelina drummondi (Thompson, 1844)				Ballesteros (1984)
Facelina sp.				Ballesteros (1984)

Familia FAVORINIDAE			
Favorinus branchialis (Rathke, 1806): bajo piedras, zona detrítica, i		+	v
***Favorinus vitreus* (Ortea, 1982)**: bajo piedras, zona detrítica, i		+	v
Familia AEOLIDIDAE			
Aeolidiella alderi (Cocks, 1852)		Ros (1975)	
Berghia verrucicornis (O. G. Costa, 1864): bajo piedras, zona detrítica, i		+++	v
Spurilla neapolitana (delle Chiaje, 1841): bajo piedras, zona detrítica, i		+++	v
Familia SIPHONARIIDAE			
Williamia gussonii (O. G. Costa, 1829): zonas detríticas, i		++	
Familia TRIMUSCULIDAE			
Trimusculus mammilaris (Linnaeus, 1758): i		+++	
Familia ELLOBIIDAE			
Auriculinella erosa (Jeffreys, 1829)		++	
Ovatella firminii (Payraudeau, 1826)		++	
Ovatella myosotis (Draparnaud, 1801)		+++	
Clase BIVALVIA			
Familia NUCULIDAE			
Nucula hanleyi Winckworth, 1930: fango, c		+++	v, Aa
Nucula nitidosa Winckworth, 1930: fango y detrito coralígeno, c-b		+++	(p), v, Aa
***Nucula* cfr. *nucleus* (Linnaeus, 1758)**: fango, c		+++	v, Aa
Nucula sulcata Bronn, 183: fango y detrito coralígeno, c-b		+++	(p), v, Aa
**Ennucula aegeensis* (Forbes, 1844): fango y detrito coralígeno, c-b		+++	(p), v, Ai
Familia NUCULANIDAE			
Nuculana commutata (Philippi, 1844): fango y detrito coralígeno, c-b		++++	(p), Ai
Nuculana pella (Linnaeus, 1767): fango, c		++	Aa
Familia YOLDIIDAE			
****Yoldiella lucida* (Lovén, 1846)**: b	Fig. 86	++	p, Ai
****Yoldiella nana* (M. Sars, 1865)**: fango y detrito coralígeno, b	Fig. 87	++	(p), Ai
****Yoldiella philippiana* (Nyst, 1845)**: fango y detrito coralígeno, b	Figs. 88-93	+++	(p), v, Ai
Familia ARCIDAE			
Arca noae Linnaeus, 1758: rocas, i		++	v
Arca tetragona Poli, 1795		+	
Barbatia barbata (Linnaeus, 1758): rocas, i		++	v
Barbatia clathrata (Defrance, 1816): b		++	p
Anadara diluvii (Lamarck, 1819): fango, c		+++	v
Bathyarca pectunculoides (Scacchi, 1834): b	Fig. 94	+++	(p), v
Bathyarca philippiana (Nyst, 1848): b	Fig. 95	+++	(p)
Familia NOETIIDAE			
Striarca lactea (Linnaeus, 1758): piedras, i-c		+++	v
Familia GLYCYMERIDAE			
Glycymeris glycymeris (Linnaeus, 1758): fango, c		++	v
Glycymeris insubrica (Brocchi, 1814): arena, i		+++	v
Familia MYTILIDAE			
Mytilus galloprovincialis Lamarck, 1819: rocas y espigones, i		++++	v
Mytilaster minimus (Poli, 1795): rocas, m		++++	v
**Crenella pellucida* (Jeffreys, 1850): detrito coralígeno, b	Fig. 96	++	p, v
Gregariella subclavata (Libassi, 1859): rocas, i		+++	v
Gregariella petagnae (Scacchi, 1832): rocas, i		+++	v
Musculus costulatus (Risso, 1826)		+++	
Musculus subpictus (Cantraine, 1835): fango, c		++	v
Lithophaga lithophaga (Linnaeus, 1758): en piedras, i-c		++	v
Modiolus adriaticus Lamarck, 1819		+	
Modiolus barbatus (Linnaeus, 1758): rocas, i		+++	

Idas* **cfr. ***ghisottii*** **Warén y Carrozza, 1990**: madera		+	
****Idas simpsoni*** **(Marshall, 1900)**: esqueletos de peces y cetáceos, i-c		++	
Modiolula phaseolina **(Philippi, 1844)**: detrito coralígeno, b	Fig. 97	++++	p, (f), v
Familia PINNIDAE			
Atrina pectinata (Linnaeus, 1758): fango, c		+++	v
Pinna nobilis Linnaeus, 1758: praderas de *Posidonia*, i		+	
Familia PTERIIDAE			
Pteria hirundo (Linnaeus, 1758): gorgonias y restos de redes, c		+++	v
Familia PECTINIDAE			
Palliolum incomparabile (Risso, 1826)		++	
Delectopecten vitreus (Gmelin, 1791): b		++	p
Pseudamussium septemradiatum **(O. F. Müller, 1776)**: fango, c		++	(p), (f), v
Peplum clavatum (Poli, 1795): fango, c		+++	(p), v
Karnekampia bruei (Payraudeau, 1826): b		+	p
Manupecten pesfelis (Linnaeus, 1758): c-b		++	(p)
Chlamys islandica (O. F. Müller, 1776)		+++	(p), f
Chlamys multistriata (Poli, 1795): fango, i-c		++	v
Chlamys varia (Linnaeus, 1758): roca y fango, i-c		+++	v
Lissopecten hyalinum (Poli, 1795)		++	v
Flexopecten flexuosus (Poli, 1795): arena y fango, i-c		+++	v
Flexopecten glaber **(Linnaeus, 1758)**		+	
Aequipecten opercularis (Linnaeus, 1758): fango, c		+++	(p), (f), v
Perapecten commutatus (Monterosato, 1875): fango, c		++	v
Pecten jacobaeus (Linnaeus, 1758): arena y fango, i-c		++++	v
Similipecten similis (Laskey, 1811): fango y detrito coralígeno, c-b		++	(p), v, Ai
**Propeamussium lucidum* (Jeffreys in Thompson, 1873): detrito coralígeno, b		+	p
Propeamussium fenestratum (Forbes, 1844): detrito coralígeno, b		+	p
**Cyclopecten hoskynsi* (Forbes, 1844): detrito coralígeno, b		+	p
Familia SPONDYLIDAE			
Spondylus gaederopus Linnaeus, 1758		++	
Familia ANOMIIDAE			
Anomia ephippium Linnaeus, 1758: conchas de moluscos		+++	v
**Heteranomia squamula* (Linnaeus, 1758): b		++	(p), v
Monia patelliformis (Linnaeus, 1761)		++	
Familia LIMIDAE			
Limaria hians (Gmelin, 1791): rocas y espigones, i		+++	v
Limaria inflata Link, 1807: i		++	
Notolimea crassa (Forbes, 1844): detrito coralígeno, b		++	p
Limatula subauriculata (Montagu, 1808): detrito coralígeno, b		++	p
****Limatula*** **cfr.** ***gwyni*** **(Sykes, 1903)**: detrito coralígeno, b		+	p
Familia OSTREIDAE			
Ostrea edulis Linnaeus, 1758: rocas, i		+++	v
Familia GRYPHAEIDAE			
Neopycnodonte cochlear (Poli, 1795): c-b		++	(p)
Familia LUCINIDAE			
Ctena decussata (O. G. Costa, 1829): arena, i		+++	v
Loripes lacteus (Linnaeus, 1758): arena, i		++++	v
Lucinella divaricata (Linnaeus, 1758): arena, i		+++	v
Lucinoma borealis **(Linnaeus, 1767)**: fango y detrito coralígeno. c-b		++	(p), v
Myrtea spinifera (Montagu, 1803): i		++	
Familia THYASIRIDAE			
Thyasira (Thyasira) biplicata **(Philippi, 1836)**: b	Fig. 98	++	p
**Thyasira (Thyasira) obsoleta* (Verrill y Bush, 1898): b	Fig. 99	++	p
**Thyasira (Parathyasira) granulosa* (Mont., 1874 ex Jeffreys): b	Figs. 101, 102	+	p

**Thyasira (Parathyasira) subovata* (Jeffreys, 1881): detrito coralígeno, b	Fig. 100	+++	p, v
**Thyasira (Leptaxinus) incrassata* (Jeffreys, 1876): b	Fig. 103	++	(p)
**Thyasira (Axinulus) croulinensis* (Jeffreys, 1847): b	Fig. 104	++	p
**Thyasira (Axinulus) eumyaria* (M. Sars, 1870): b	Fig. 105	++	p
Thyasira (Mendicula) ferruginea (Locard, 1886): fango y detrito coralígeno, b	Fig. 106	+++	(p), v
Familia CHAMIDAE			
Chama gryphoides Linnaeus, 1758: en piedras o *Microccosmus*, i		+++	v
Pseudochama gryphina (Lamarck, 1819): rocas, i		+	
Familia ERYCINIDAE			
Scacchia ovata Philippi, 1844: i		++	
Familia KELLIIDAE			
Bornia sebetia (O. G. Costa, 1829): i		+++	
Kellia suborbicularis (Montagu, 1803): b		++	(p), v
Familia LASAEIDAE			
Hemilepton nitidum (Turton, 1822): b		++	(p)
Familia MONTACUTIDAE			
**Mancikellia pumila* (Sowerby, 1846): b		++++	p
**Montacuta phascolionis* Dautzenberg y Fischer, 1925: b		+	p
Montacuta substriata (Montagu, 1808): b		++	(p)
Mysella bidentata (Montagu, 1803): i		+++	v
Mysella obliquata (Chaster, 1897)		++	
Tellimya ferruginosa (Montagu, 1808): b		+	p
***Epilepton clarkiae* (Clark, 1852)**: b		++	p
***Epilepton* sp.:** detrito coralígeno, b		+++	p, v
Familia NEOLEPTONIDAE			
****Arculus* sp.:** detrito coralígeno, b	Fig. 107	++	p
Familia CARDITIDAE			
Venericardia antiquata (Linnaeus, 1758): fango, c		+++	v
Glans aculeata (Poli, 1795): fango y detrito coralígeno, c-b		++++	(p), v
Glans trapezia (Linnaeus, 1758): fango y piedras, c		+++	v
Familia ASTARTIDAE			
Astarte fusca (Poli, 1795): fango, c		++	v
Astarte sulcata (da Costa, 1778): fango, c		++	v
Goodallia triangularis (Montagu, 1803): i. b		+	(p)
***Goodallia* sp**.: detrito coralígeno, b		++	p
Familia CARDIIDAE			
Acanthocardia aculeata (Linnaeus, 1758): arena, i		+++	v
Acanthocardia echinata (Linnaeus, 1758): fango, c		++	v
Acanthocardia paucicostata (Sowerby, 1834): fango, i-c		+++	v
Acanthocardia tuberculata (Linnaeus, 1758): arena, i		++++	v
Parvicardium exiguum (Gmelin, 1791): i		++	v
Parvicardium minimum (Philippi, 1836). fango y detrito coralígeno, c-b		+++	(p), v, Ai
Parvicardium ovale (G. B. Sowerby, 1840): i		++	v
Parvicardium roseum (Lamarck, 1819): fango, c		+	v, Aa
Plagiocardium papillosum (Poli, 1795): arena, i		++	v
Laevicardium crassum (Gmelin, 1791): fango, c		++	v
Laevicardium oblongum (Chemnitz, 1782): fango, c-b		+++	v
Cerastoderma glaucum (Poiret, 1789): arena fangosa, i		+++	v
Familia MACTRIDAE			
Mactra glauca (Born, 1778): arena, i		+	
Mactra stultorum (Linnaeus, 1758): arena, i		++++	v, Aa
Spisula subtruncata (da Costa, 1778): arena, i		++++	v, Aa
Lutraria angustior Philippi, 1844		+	
Lutraria lutraria (Linnaeus, 1758): i-c		+++	v
Lutraria magna (da Costa, 1778): *Posidonia* y fango, i-c		++	v

Familia MESODESMATIDAE		
Donacilla cornea (Poli, 1795)	+	v
Ervilia castanea (Montagu, 1803): fango, c	++	v, Ai
Familia SOLENIDAE		
Solen marginatus Pulteney, 1799: fango, i	+++	v
Familia PHARIDAE		
Ensis ensis (Linnaeus, 1758): arena, i	+++	v
Ensis minor (Chenu, 1843): arena, i	+++	v
Pharus legumen (Linnaeus, 1758): arena, i	+++	v
Familia TELLINIDAE		
Arcopagia balaustina (Linnaeus, 1758): fango, c-b	++	(p), v, Aa
Arcopagia crassa (Pennant, 1777): fango y rocas, i-c	+++	v
Gastrana fragilis (Linnaeus, 1758)	+++	v
Macoma cumana (O. G. Costa, 1829): arena, i	+++	v
Tellina donacina Linnaeus, 1758: arena y fango, i-c	+++	v
Tellina incarnata Linnaeus, 1758: arena, i	++++	v
Tellina nitida Poli, 1791: arena, i	++++	v
Tellina planata Linnaeus, 1758: arena, i	++++	v
Tellina pulchella Lamarck, 1818: arena y fango, i-c	+++	v
Tellina serrata Brocchi, 1814: fango, c-b	+++	(p), v
Tellina tenuis da Costa, 1778: arena, i	++++	v
Familia DONACIDAE		
Donax semistriatus Poli, 1795: arena, i	+++	v
Donax trunculus Linnaeus, 1758: arena, i	++++	v
Familia PSAMMOBIIDAE		
Gari fervensis (Gmelin, 1791)	++	
Familia SCROBICULARIIDAE		
Scrobicularia cottardi (Payraudeau, 1826)	+++	
Familia SEMELIDAE		
Abra longicallus (Scacchi, 1834): detrito coralígeno, b	++	(p), v
Familia SOLECURTIDAE		
Solecurtus scopula (Turton, 1822): fango, c	++	v
Solecurtus strigilatus (Linnaeus, 1758): fango, c	+++	v
Azorinus chamasolen (da Costa, 1778): fango, c	++	v
Familia ARCTICIDAE		
Arctica islandica (Linnaeus, 1767)	++	p, f
Familia KELLIELLIDAE		
Kelliella abyssicola (Forbes, 1844): fango, c-b	++++	(p), v, Ai
Familia TRAPEZIIDAE		
Coralliophaga lithophagella (Lamarck, 1819): rocas, c	+	v
Familia GLOSSIDAE		
Glossus humanus (Linnaeus, 1758): fango, c	+++	v
Familia VENERIDAE		
Callista chione (Linnaeus, 1758): arena, i	+++	v
Chamelea gallina (Linnaeus, 1758): arena, i	++++	v
Clausinella fasciata (da Costa, 1778): fango, c	++	v, Aa
Dosinia exoleta (Linnaeus, 1758): fango, c	+++	v
Dosinia lupinus (Linnaeus, 1758): arena y fango, i-c	+++	v
Globivenus effosa (Bivona, 1836)	++	p, f
Gouldia minima (Montagu, 1803): b	++	(p), v
Irus irus (Linnaeus, 1758): interior de piedras calcáreas, m-i	++++	v
Paphia aurea (Gmelin, 1791): i	+++	v
Paphia rhomboides (Pennant, 1777): fango, i-c	+++	v
Pitar mediterranea Tiberi, 1855: b	+++	p

Pitar rudis (Poli, 1795): fango, c-b		++	(p), v, Aa
Tapes decussatus (Linnaeus, 1758): arena fangosa, i		+++	v
Timoclea ovata (Pennant, 1777): fango, c-b		++++	(p), v, Aa
Venerupis corrugata (Gmelin, 1791): arena, i		+++	v, Aa
Venus casina Linnaeus, 1758: fango, c		++	v
Venus nux Gmelin, 1791		++	v
Venus verrucosa Linnaeus, 1758: fango, c		+++	v
Familia PETRICOLIDAE			
Petricola lithophaga (Retzius, 1786): interior de piedras calcáreas, m-i		+++	v
Mysia undata (Pennant, 1777): fango, i-c		++	v
Familia CORBULIDAE			
Corbula gibba (Olivi, 1792): fango y detrito coralígeno, c-b		+++	(p), v, Aa
Lentidium mediterraneum (O. G. Costa, 1829): arena, i		++	v
Familia GASTROCHAENIDAE			
Gastrochaena dubia (Pennant, 1777): interior de piedras calcáreas, i		++	v
Familia HIATELLIDAE			
Hiatella arctica (Linnaeus, 1767): restos de conchas y piedras, i-c		+++	v
Hiatella rugosa (Linnaeus, 1767): restos de conchas, piedras y detrito coralígeno, i-b		▲++	(p), v
Panopea norvegica (Spengler, 1793)		+	p, f
Familia PHOLADIDAE			
Barnea candida (Linnaeus, 1758): arena con bloques de fango, i		+++	v
Pholas dactylus Linnaeus, 1758: arena y fango, i		+++	v
Familia TEREDINIDAE			
*_Bankia carinata_ (Gray, 1827): madera	Fig. 109	++	v
*_Lyrodus pedicellatus_ (Quatrefages, 1849): madera	Fig. 110	+++	v
Nototeredo norvegica (Spengler, 1792): madera	Fig. 111	+++	v
Familia XYLOPHAGIDAE			
Xylophaga dorsalis (Turton, 1819): madera y detrito coralígeno	Fig. 108	+++	(p), v
Familia THRACIIDAE			
Thracia convexa (Wood, 1815): fango, c		++	v
Thracia corbuloides Deshayes, 1830: fango, c		++	v
Thracia papyracea (Poli, 1795): arena, i		+++	
Thracia pubescens (Pulteney, 1799): fango, c		+++	v
Familia PANDORIDAE			
Pandora inaequivalvis (Linnaeus, 1758): arena, i		+++	v
Pandora pinna (Montagu, 1803): fango y detrito coralígeno, b		++	p, v
Familia POROMYIDAE			
Poromya granulata (Nyst y Westendorp, 1839): fango y detrito coralígeno, b		+	p, Ai
Familia CUSPIDARIIDAE			
*_Cardiomya striolata_ (Locard, 1898): fango y detrito coralígeno, b		++	p, v, Ai
*_Cuspidaria abbreviata_ (Forbes, 1843): b		+	p
Cuspidaria cuspidata (Olivi, 1792): b		++	v
Cuspidaria rostrata (Spengler, 1793): b		++	(p), v
Clase SCAPHOPODA			
Familia DENTALIIDAE			
Dentalium agile Sars, 1872		++	
Dentalium inaequicostatum Dautzenberg, 1891: fango y detrito coralígeno, c-b		++++	(p), v, Ai
Dentalium panormum Chenu, 1842: b		+++	p
Dentalium vulgare da Costa, 1778: arena y detrito rocoso, i		+++	v
Fustiaria rubescens (Deshayes, 1825): i		++	
Familia SIPHONODENTALIIDAE			
Pulsellum lofotense (Sars, 1865): fango y detrito coralígeno, b		++	(p), v, Ai
Cadulus jeffreysi (Monterosato, 1875): b		++	p
Entalina tetragona (Brocchi, 1814): b		++++	p

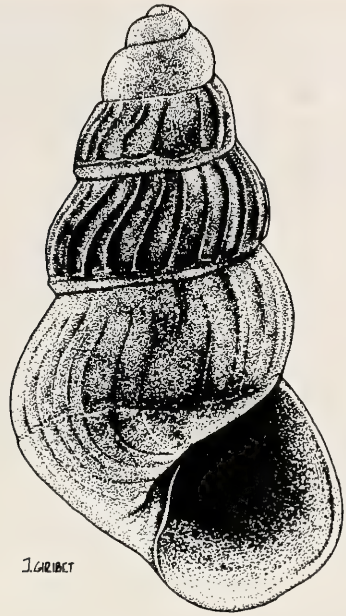


Figura 2. Concha de *Rissoa gemmula* (Sitges, 1,7 mm).
Figure 2. Shell of Rissoa gemmula *(Sitges, 1.7 mm).*

DISCUSIÓN

COMENTARIOS SOBRE ALGUNOS TÁXONES: De la mayoría de especies citadas para el Garraf existen fotografías y descripciones actualizadas en la literatura, aunque algunas un poco dispersas. En este apartado nos hemos limitado a comentar algunos de los taxones que nos han parecido de mayor interés, ya sea por su rareza, por su importancia pesquera-comercial en el Garraf, por la escasa documentación bibliográfica existente, o bien por su importancia biológica en la zona. De muchas de estas especies reportamos fotografías, la mayoría al M.E.B., de la concha o de la protoconcha, según convenga para su identificación.

Clase GASTROPODA
Familia LEPETIDAE

Iothia fulva (O. F. Müller, 1776)

Esta especie atlántica ha sido citada para el Mediterráneo por TAVIANI (1974), más concretamente para el Adriático, en fondos de fango entre 180 y 320 m de profundidad, aunque como comenta el propio autor, seguramente se trataba de una concha semifósil del Würmiense. CECALUPO Y GIUSTI (1986) citan otro ejemplar en buenas condiciones de la Isla de Capraia, entre 400 y 440 m de profundidad. Nuestro único ejemplar también parece ser un fósil Würmiense, puesto que se trata de una concha mal conservada, procedente del detrito de "El Parrusset" entre 250 y 350 m de profundidad.

Familia LEPETELLIDAE

Lepetella cfr. *espinosae* Dantart y Luque, 1994

No se han encontrado ejemplares vivos de esta especie, y la diagnosis sólo es posible estudiando la morfología del animal. De todas formas las otras dos especies con las que podría confundirse, *Lepetella sierrai* Dantart y Luque, 1994 y *L. barrajoni* Dantart y Luque, 1994, no se han encontrado en el Mediterráneo (ver DANTART Y LUQUE, 1994).

Familia ADDISONIIDAE

Addisonia excentrica Tiberi, 1857 (Fig. 3)

MCLEAN (1985) señala que la principal diferencia entre *A. paradoxa* Dall, 1882 del Atlántico occidental, y *A. excentrica* (Tiberi, 1857) es el tamaño del adulto, dando 20, 3 mm de talla máxima para la primera y 10, 5 mm para la segunada. DANTART Y LUQUE (1994), tras una detallada discusión, consideran a *A. paradoxa* sinónimo posterior de *A. excentrica*, y reportan ejemplares de esta última de hasta 12 mm. Nosotros hemos encontrado un ejemplar de *A. excentrica* de 20 mm, por lo que ratificamos esta sinonimia.

Familia FISSURELLIDAE

Emarginula pustula Thiele in Kuester, 1913 (Fig. 4)

Esta especie ha sido considerada por PIANI (1984) como un "endemismo del archipiélago Toscano y de la costa Sarda oriental", pero el hallazgo de un ejemplar en el detrito de "El Parrusset", amplía su distribución al Mediterráneo occidental, hecho éste que era de esperar.

Familia SCISSURELLIDAE

Anatoma aspera (Philippi, 1844)

Esta especie ha sido considerada sinónina de *A. crispata* Fleming, 1828, o como una subespecie de ésta (SCHIRÒ, 1986), pero presenta una espira más alta, y parece ser que *A. crispata* no vive al sur de Escocia (Gofas, *com. pers.*), y además ambas especies presentan diferencias en la rádula (DANTART, *com. pers.*).

Familia RISSOIDAE

Alvania cimicoides (Forbes, 1844) y *Alvania testae* (Aradas y Maggiore, 1843) (Figs. 7, 9, 10)

Los miles de ejemplares de *A. testae* hallados en los contenidos estomacales de *Astropecten irregularis*, contrastan con los tan sólo cuatro de *A. cimicoides* (hallados todos ellos en la misma estrella), a pesar de que en sedimentos como el de "El Parrusset" *A. cimicoides* es aproximadamente tres veces más frecuente que *A. testae*.

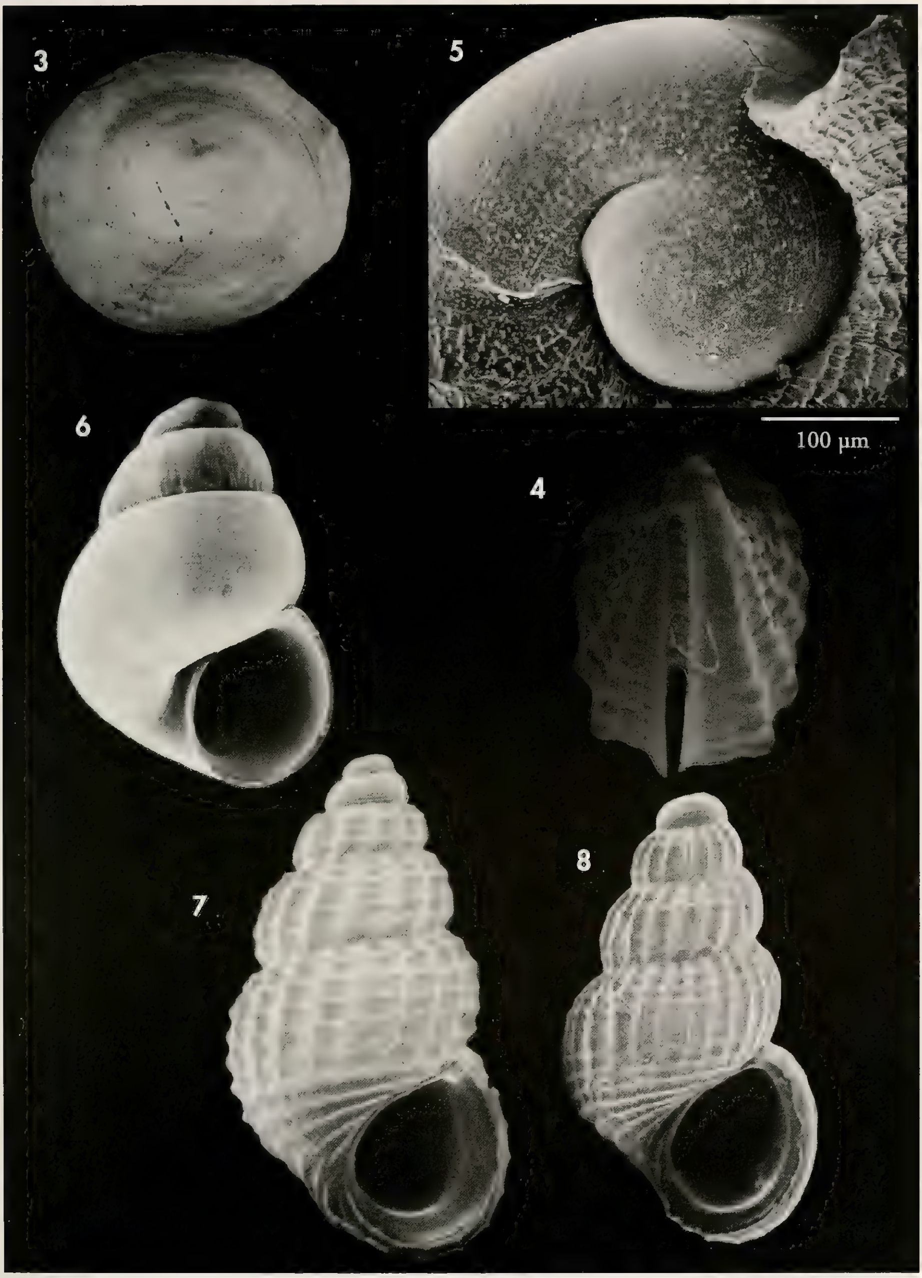


Figura 3. *Addisonia excentrica* (El Parrusset), 20 mm. Figura 4. *Emarginula pustula* (El Parrusset), 1,22 mm. Figura 5. Protoconcha de *Danilia otaviana* (El Parrusset). Figura 6. *Obtusella macilenta* (Vilanova). Figura 7. *Alvania testae* (Vilanova), 2,16 mm. Figura 8. *Alvania subsoluta* (isla de Capraia, Italia), 2,1 mm.

Figure 3. Addisonia excentrica *(El Parrusset), 20 mm. Figure 4.* Emarginula pustula *(El Parrusset), 1.22 mm. Figure 5. Protoconch of* Danilia otaviana *(El Parrusset). Figure 6.* Obtusella macilenta. *(Vilanova). Figure 7.* Alvania testae *(Vilanova), 2.16 mm. Figura 8.* Alvania subsoluta *(Capraia Island, Italy), 2.1 mm.*

Alvania zylensis Gofas y Warén, 1982 (Figs. 13, 14)

Esta especie fue descrita por GOFAS Y WARÉN (1982) para las costas atlánticas de Marruecos. AARTSEN, MENKHORST Y GITTENBERGER (1984) la citan en la Bahía de Algeciras, y posteriormente, BOGI, COPPINI Y MARGELLI (1989) la mencionan por primera vez para el Mediterráneo, en el Tirreno. En el detrito de "El Parrusset" hemos encontrado algunas conchas que asociamos a esta especie, concretamente a la forma de profundidad descrita por BOGI *ET AL.* (1989), que presenta una teleoconcha con una escultura débil. El diámetro máximo de la protoconcha es de 530 mm. Aportamos, además, la fotografía de un ejemplar de la Isla de Alborán (Fig. 14), que aunque presenta una teleoconcha idéntica a la de los ejemplares de Vallcarca, tiene una protoconcha más pequeña, de 450 mm de diámetro.

Obtusella macilenta (Monterosato, 1880) (Fig. 6)

Es una especie abundante en todos los fondos fangosos del Garraf, mientras que sólo hemos hallado unos pocos ejemplares de *O. intersecta* (Wood, 1857). Sin embargo, lo normal en fondos similares de otras regiones es que la proporción sea inversa.

Rissoa gemmula Fischer in de Folin, 1871 (Figs. 2, 20, 21)

Se han encontrado dos conchas en el litoral de Sitges, más una en Es Caló (Formentera, Islas Baleares). Aunque no se ha estudiado el material tipo, los tres ejemplares se corresponden con la descripción aparecida en FOLIN (1871), que reproducimos a continuación, y con la figura representada en NORDSIECK (1972):

"... Long $1^{1}/_{3}$ millim. Coquille conique-allongée, blanche, subdiaphane, ornée de côtes longitudinales obsolètes, à peine indiquées, et de stries spirales, visibles a la partie inférieure des tours. Sept tours de spire ventrus: les trois premiers translucides, brillants, globuleux, papilliformes; le quatrième dilaté, proportionnellement trés large; les dernieurs peu dilatés; suture bordée, ornée en dessous d'une petite zone transverse, brune, interrompue de blanc; dernier tour orné, a sa partie moyenne, d'une zonule de même coloration; overture petite, ovale; periostoma simple. Observation. - On ne pourrait rapprocher ce *Rissoa* que du *R. dolium* (Nyst), (*Nassa* Philippi); mais notre espèce est plus élancée, plus petite, à côtes obsolètes, et sa coloration est spéciale, comme la présence de la zone suturale et de la zone médiane du dernier tour".

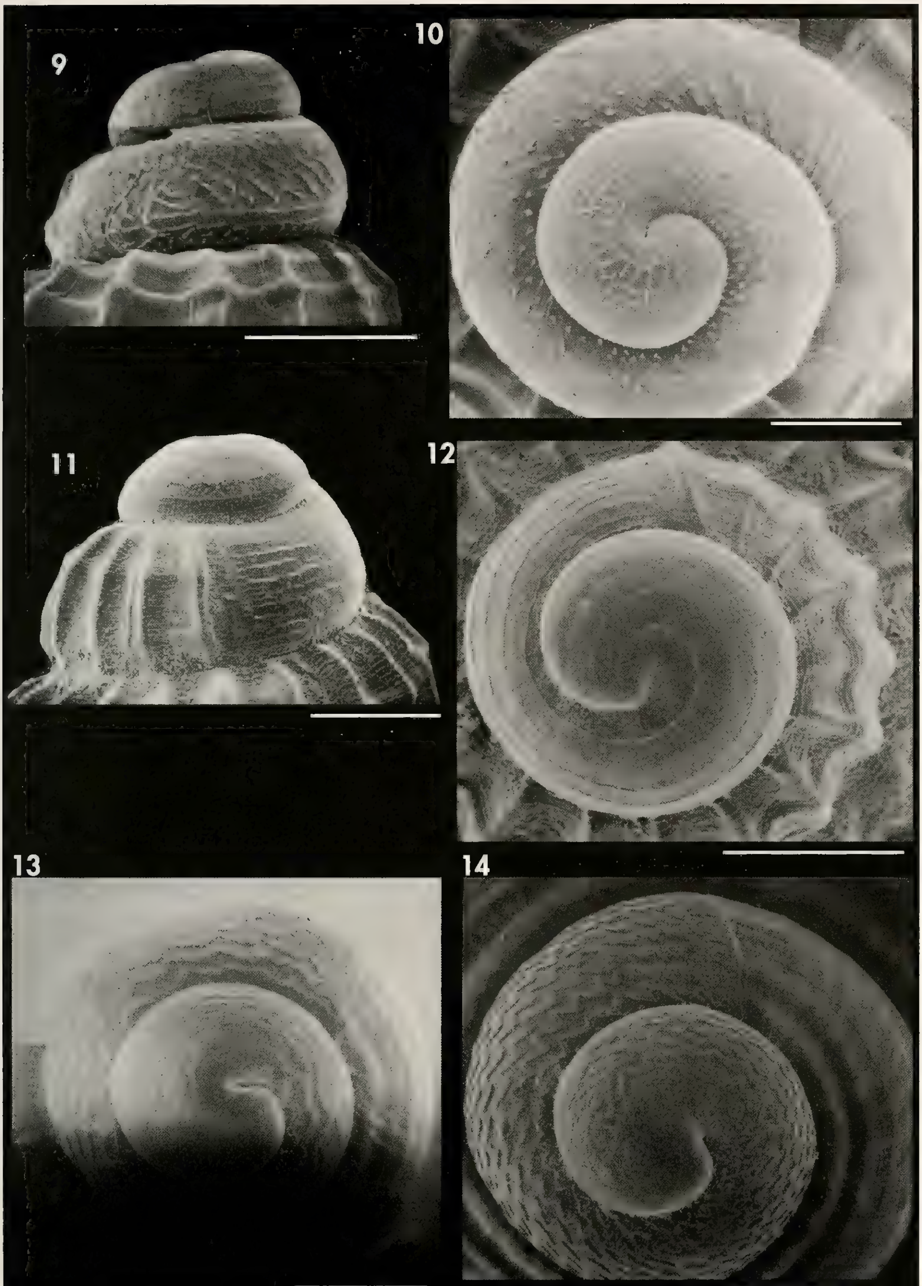
En cuanto a la protoconcha, es lisa de $2^{1}/_{4}$ vueltas de espira, con un diámetro máximo de 390 mm. Hemos incluído en el trabajo un dibujo detallado de la concha (Fig. 2), aparte de las fotografías realizadas al M.E.B. (Figs. 20, 21).

Además, hemos fotografiado las especies de Rissoidae a nuestro juicio más cercanas, *Pusillina inconspicua* (Alder, 1844) (Figs. 17-19) y *P. philippi* (Aradas y Maggiore, 1844) (Figs. 15, 16), de las que se diferencia por la coloración y forma.

Familia CALYPTRAEIDAE

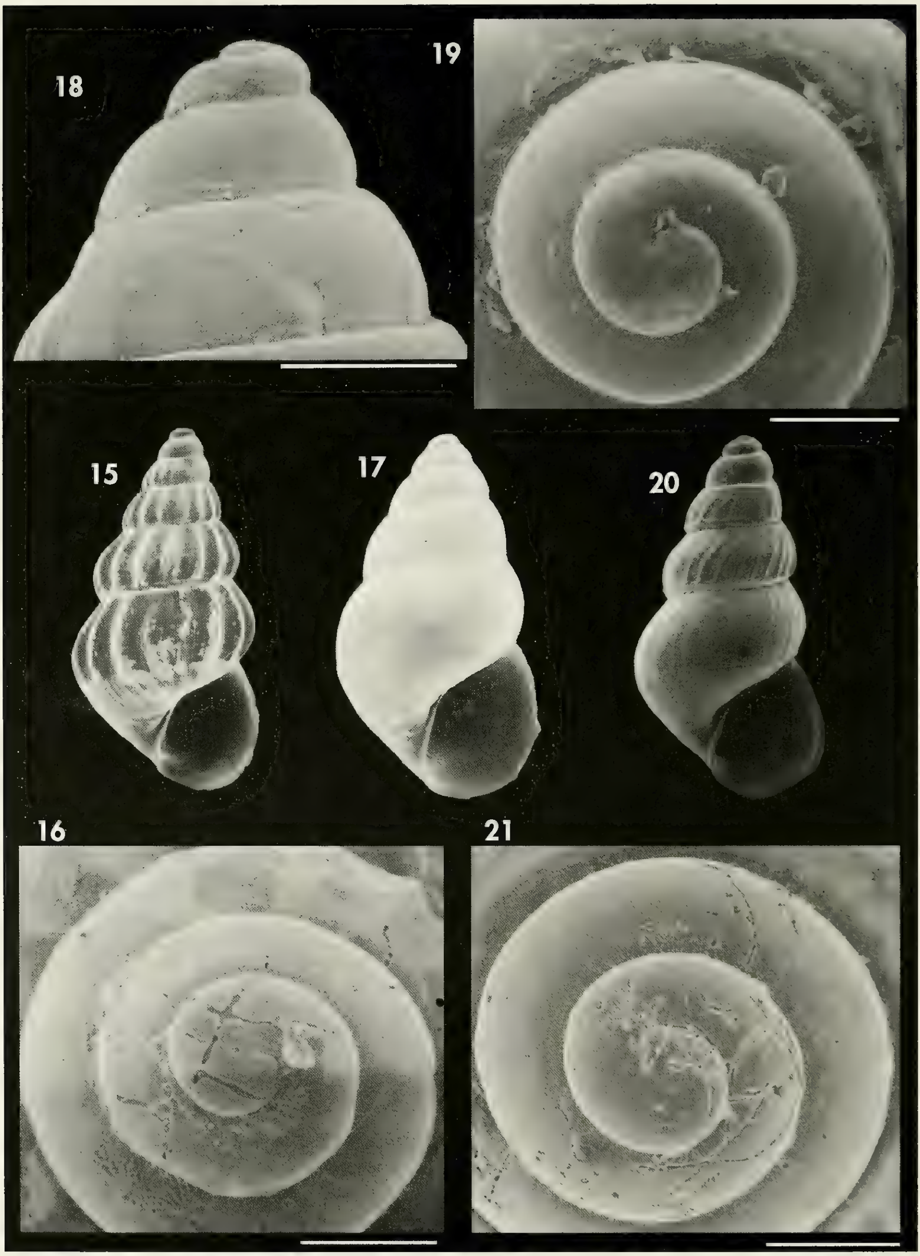
Crepidula fornicata (Linnaeus, 1758)

Aunque se ha hallado una única concha, su presencia en la zona puede explicarse por la introducción artificial adherida al casco de un barco. Además, en el puerto de Barcelona (a tan sólo 45 km de distancia) han aparecido numerosos ejemplares vivos de esta especie.



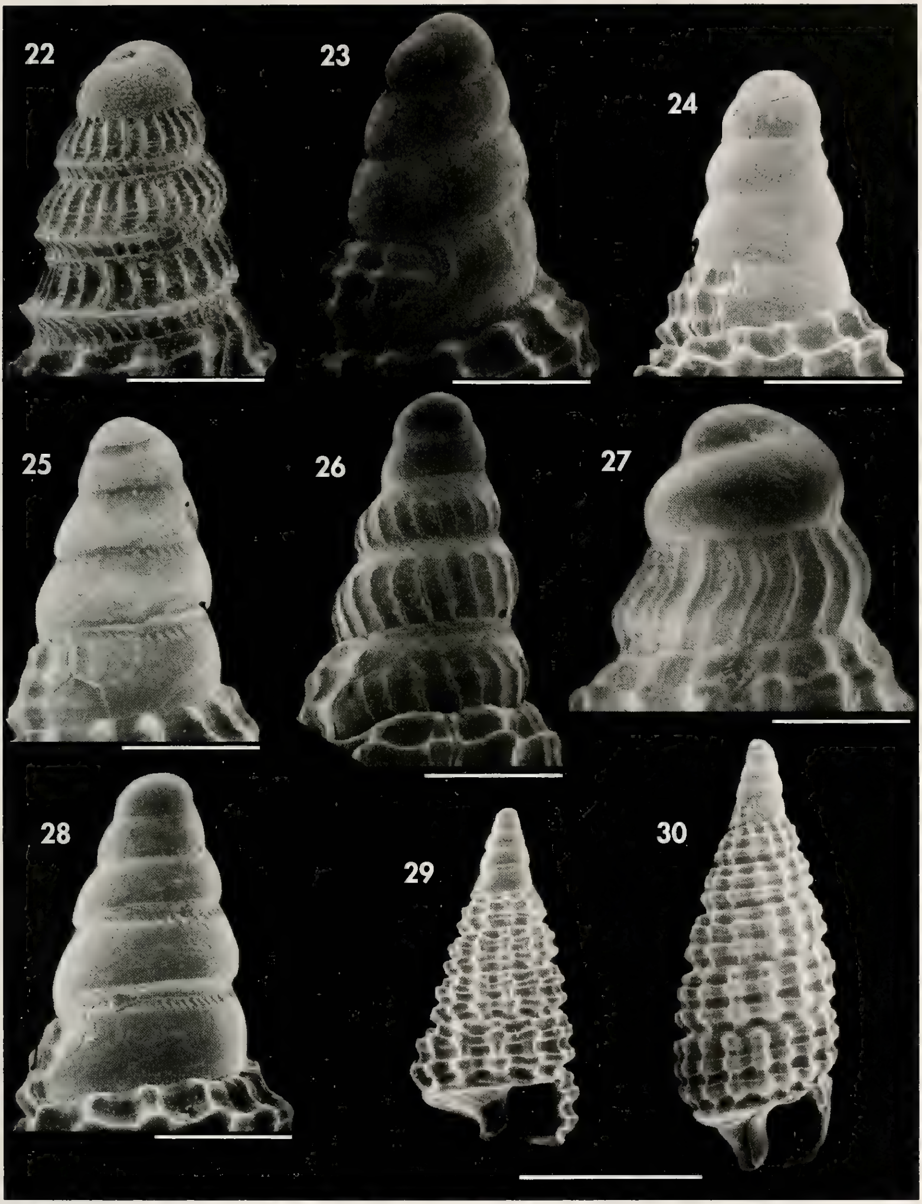
Figuras 9-14. Género *Alvania*, protoconchas. 9, 10: *A. testae* (Vilanova); 11, 12: *A. subsoluta* (isla de Capraia, Italia); 13: *A. zylensis* (El Parrusset); 14: *A. zylensis* (isla de Alborán). Escalas, 9, 11-14: 200 µm; 10: 100 µm.

Figures 9-14. Genus Alvania, *protoconchs. 9, 10:* A. testae *(Vilanova); 11, 12:* A. subsoluta *(Capraia Island, Italy); 13:* A. zylensis *(El Parrusset); 14:* A. zylensis *(Alborán Island). Scale bars, 9, 11-14: 200 µm; 10: 100 µm.*



Figuras 15, 16. *Pusillina philippi* (cala Montjoy, Roses, Girona). 15: ejemplar de 2,1 mm; 16: protoconcha. Figuras 17-19. *Pusillina inconspicua* (Tossa de Mar, Girona). 17: ejemplar de 1,7 mm; 18, 19: protoconcha. Figuras 20, 21. *Rissoa gemmula* (Sitges). 20: ejemplar de 1,7 mm; 21: protoconcha. Escalas, 16, 19, 21: 100 µm; 18: 200 µm.

Figures 15, 16. Pusillina philippi *(cala Montjoy, Roses, Girona). 15: shell of 2.1 mm; 16: protoconch. Figures 17-19.* Pusillina inconspicua *(Tossa de Mar, Girona). 17: shell of 1.7 mm; 18, 19: protoconch. Figures 20, 21.* Rissoa gemmula *(Sitges). 20: shell of 1.7 mm; 21: protoconch. Scale bars: 16, 19, 21: 100 µm; 18: 200 µm.*



Figuras 22-28. Protoconchas de *Cerithiopsis*. 22: *C. diadema* (Isla de Alborán); 23: *C. jeffreysi* (bahía de Almería); 24: *C. minima* (Sitges); 25: *C. nana* (Sitges); 26: *C. scalaris* (bahía de Almería); 27: *C. tiara* (isla de Alborán); 28: *C. tubercularis* (La Herradura, Granada). Figura 29: *C. nana* (Sitges), concha de 1,8 mm. Figura 30: *C. tubercularis* (La Herradura, Granada), concha de 2,4 mm. Escalas, 22-28: 200 µm; 29, 30: 1 mm.

Figures 22-28. Cerithiopsis *protoconchs. 22:* C. diadema *(Alborán Island); 23:* C. jeffreysi *(Almería bay); 24:* C. minima *(Sitges); 25:* C. nana *(Sitges); 26:* C. scalaris *(Almería bay); 27:* C. tiara *(Alborán Island); 28:* C. tubercularis *(La Herradura, Granada). Figure 29:* C. nana *(Sitges), shell of 1.8 mm. Figure 30:* C. tubercularis *(La Herradura, Granada), shell of 2.4 mm. Scale bars,* 22-28: 200 µm; 29, 30: 1 mm.

Familia EULIMIDAE

La familia Eulimidae es una de las más ricas en aguas profundas, quizás más que la familia Turridae (BOUCHET Y WARÉN, 1986). A diferencia de otras regiones, la zona de estudio es pobre en especies del género *Vitreolina*, que principalmente viven en aguas infralitorales. Los pocos ejemplares de este género encontrados proceden de aguas profundas.

Crinophtheiros sp. (Figs. 37, 38)

Se han encontrado tres ejemplares frescos del género *Crinophtheiros* en contenidos estomacales de *Astropecten irregularis*, a profundidades superiores a los 200 m. La especie *C. comatulicola* (Graf, 1875) es frecuente en fondos infralitorales, siempre asociada a *Antedon mediterranea* (Lamarck) (TEMPLADO, com. pers.), pero a profundidades superiores a 200 m, el crinoideo presente es *Leptometra phalangium* (Müller), por lo que podría tratarse de otra especie diferente perteneciente al género *Crinophtheiros*.

Parvioris ibizenca (Nordsieck, 1968)

La especie *Parvioris ibizenca* ha sido referida normalmente en la bibliografía como *P. microstoma* (Brusina, 1864), pero según Gofas (*com. pers.*), el nombre correcto sería el primero de éstos, porque *P. microstoma* ya está preocupado, con lo que se considera sinonimía.

Vitreolina sp.

La especie tipo del género *Vitreolina* es *Eulima incurva* Bucquoy, Dautzenberg y Dollfus, 1883, especie poco clara (BOUCHET Y WARÉN, 1986). Además, hay una gran confusión con las especies adscritas al género *Vitreolina* (eulímidos de pequeño tamaño,con forma curvada), por lo que hemos preferido mencionar estos ejemplares como *Vitreolina* sp.

Familia MURICIDAE

Trophon echinatus (Kiener, 1840) y *Trophon* sp. (Figs. 41-44)

T. echinatus presenta una considerable variación de formas de la teleoconcha, especialmente con relación a la profundidad. Sin embargo, no se ha descrito variabilidad en la protoconcha. En el detrito de "El Parrusset" hemos encontrado dos tipos de protoconcha que presentan tamaños muy diferentes; una con un diámetro máximo de unos 670 mm, que asignamos a *T. echinatus*, y otra con un diámetro máximo registrado entre 770 y 830 mm, que denominamos provisionalmente *Trophon* sp.

Trophon barvicensis (Johnston, 1825) (Fig. 45)

Según BOUCHET Y WARÉN (1985), no han visto ningún especimen mediterráneo que pueda asignarse inequívocamente a este taxón. También comentan que algunas citas de *Trophonopsis richardi* (Dautzenberg y Fischer, 1896) para el

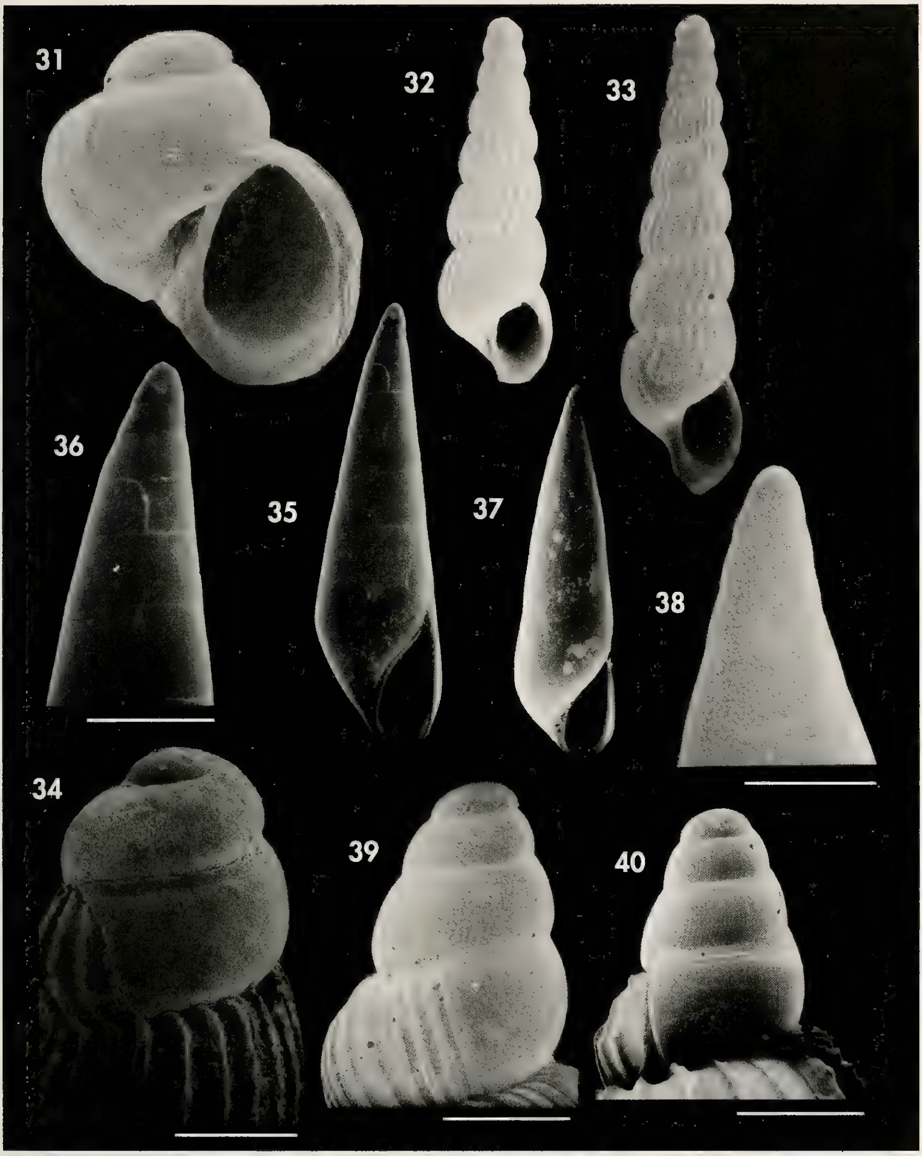
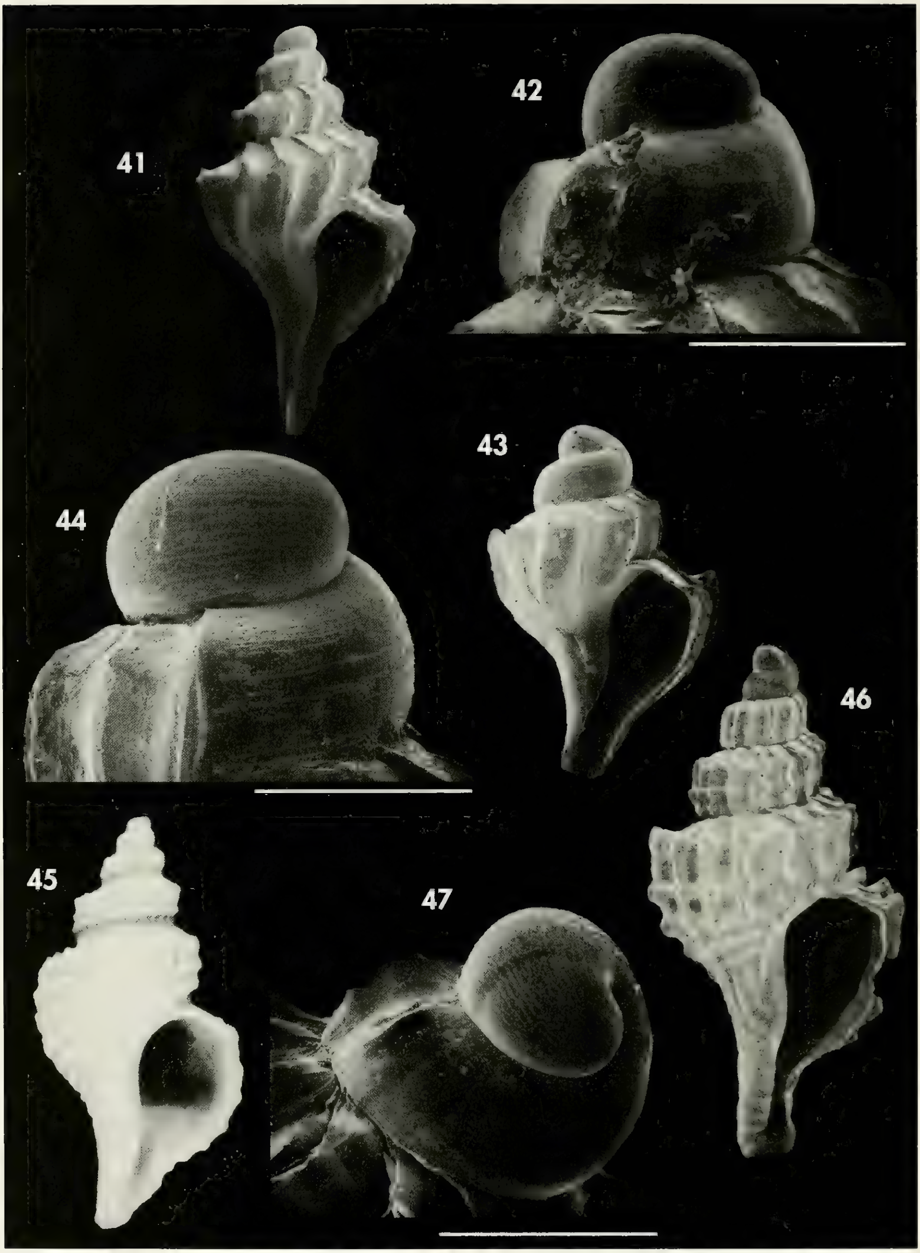
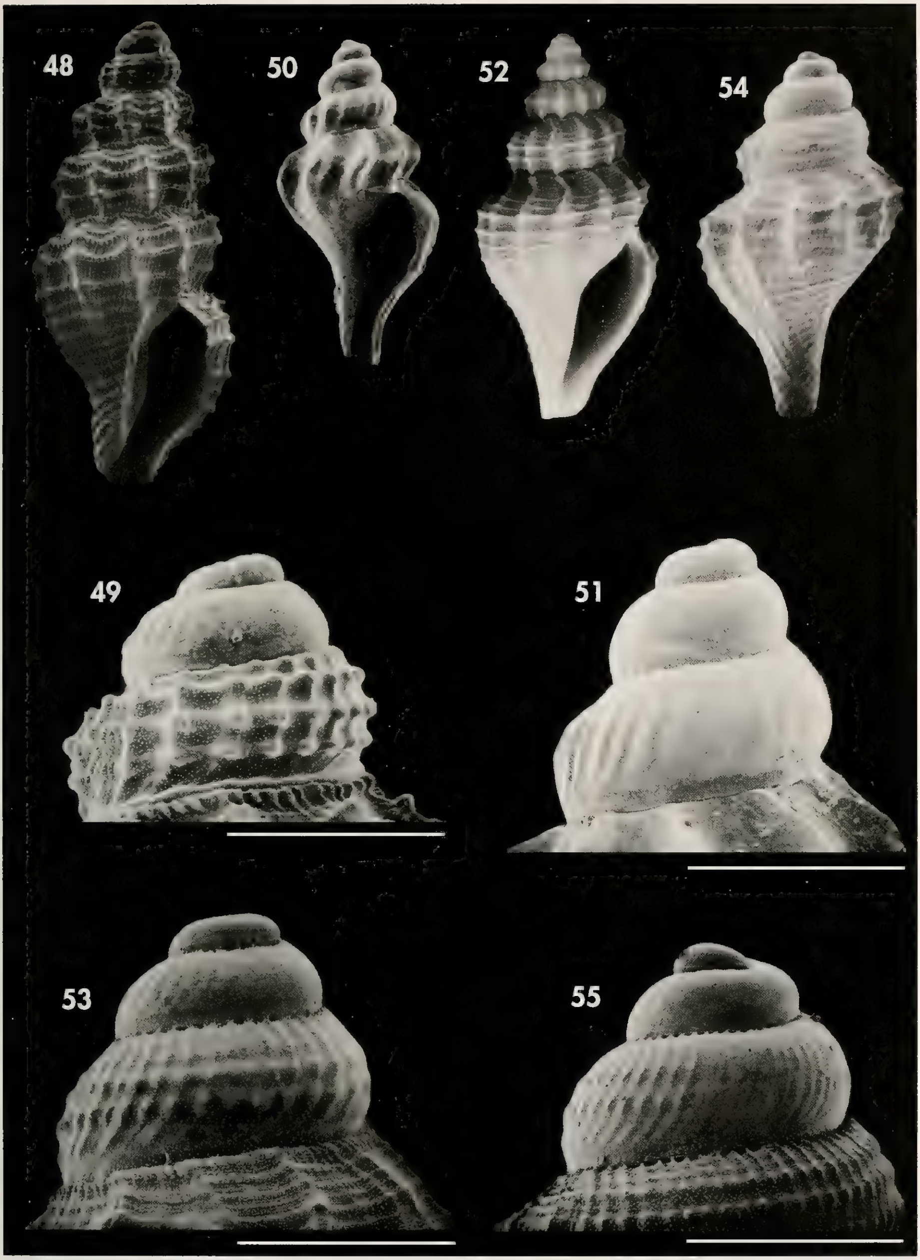


Figura 31. *Talassia dagueneti* (El Parrusset), concha juvenil de 0,88 mm. Figura 32. *Graphis albida* (El Parrusset), 1,83 mm. Figuras 33, 34. *Graphis albida* (La Herradura, Granada). 33: concha de 2,4 mm; 34: protoconcha. Figuras 35, 36. *Vitreolina perminima* (El Parrusset). 35: concha de 2,2 mm; 36: protoconcha. Figuras 37, 38. *Crinophtheiros* sp. (Vilanova). 37: concha de 4,6 mm; 38: protoconcha. Figuras 39, 40. Protoconchas de *Epitonium*. 39: *E. clathratulum* (Mijas Costa, Málaga); 40: *E. linctum* (El Parrusset). Escalas, 34: 100 µm; 36: 300 µm; 38: 300 µm; 39, 40: 200 µm.
Figure 31. Talassia dagueneti *(El Parrusset), juvenile shell of 0.88 mm. Figure 32.* Graphis albida *(El Parrusset), 1.83 mm. Figures 33, 34.* Graphis albida *(La Herradura, Granada). 33: shell of 2.4 mm; 34: protoconch. Figures 35, 36.* Vitreolina perminima *(El Parrusset). 35: shell of 2.2 mm; 36: protoconch. Figures 37, 38.* Crinophtheiros *sp. (Vilanova). 37: shell of 4.6 mm; 38: protoconch. Figures 39, 40. Protoconchs of* Epitonium. *39:* E. clathratulum *(Mijas Costa, Málaga); 40:* E. linctum *(El Parrusset). Scale bars, 34: 100 µm; 36: 300 µm; 38: 300 µm; 39, 40: 200 µm.*



Figuras 41, 42. *Trophon echinatus* (El Parrusset). 41: concha juvenil de 4,75 mm; 42: protoconcha. Figuras 43, 44. *Trophon* sp. (El Parrusset). 43: concha juvenil de 2,7 mm; 44: protoconcha. Figura 45. *Trophon barviciensis* (El Parrusset), 19 mm. Figuras 46, 47. *Trophon muricatus*. 46: concha juvenil de 5,9 mm; 47: protoconcha. Escalas 500 µm.

Figures 41, 42. Trophon echinatus *(El Parrusset). 41: juvenile shell of 4.75 mm; 42: protoconch. Figures 43, 44.* Trophon *sp. (El Parrusset). 43: juvenil shell of 2.7 mm; 44: protoconch. Figure 45.* Trophon barviciensis *(El Parrusset), 19 mm. Figures 46, 47.* Trophon muricatus. *46: juvenil shell of 5.9 mm; 47: protoconch. Scale bars 500 µm.*



Figuras 48, 49. *Bela brachystoma* (Vilanova). 48: ejemplar de 3,6 mm; 49: protoconcha. Figuras 50, 51. *Mangelia attenuata* (Vilanova). 50: ejemplar de 2,5 mm; 51: protoconcha. Figuras 52, 53. *Mangelia nuperrima* (El Parrusset). 52: ejemplar de 7 mm; 53: protoconcha. Figuras 54, 55. *Mangelia serga* (El Parrusset). 54: ejemplar de 2,75 mm; 55: protoconcha. Escalas 500 µm.
Figures 48, 49. Bela brachystoma *(Vilanova). 48: shell of 3.6 mm; 49: protoconch. Figures 50, 51.* Mangelia attenuata *(Vilanova). 50: shell of 2.5 mm; 51: protoconch. Figures 52, 53.* Mangelia nuperrima *(El Parrusset). 52: shell of 7 mm; 53: protoconch. Figures 54, 55.* Mangelia serga *(El Parrusset). 54: shell of 2.75 mm; 55: protoconch. Scale bars 500 µm.*

Mediterráneo (ver Di Geronimo y Panetta, 1973 y Franchini y Frilli, 1970), podrían corresponder a *T. barvicensis*. Nuestro único ejemplar proveniente de "El Parrusset" parece un ejemplar normal de *T. barvicensis* (Warén, com. pers.).

Familia Turridae

Mangelia costata (Donovan, 1804)

Aartsen *et al.* (1984) diferencian *M. coarctata* (Forbes, 1840) de *M. costata*, siendo la primera más grande y alargada, con una o dos costillas más y presentando una coloración uniforme. De todas maneras, dichos autores no descartan la posibilidad de que *M. costata* sea la forma litoral y *M. coarctata* la de aguas profundas de una misma especie. El análisis de más de 300 ejemplares del Mediterráneo español de la colección de uno de los autores, desde aguas someras hasta profundidades de 350 m, y cubriendo una área geográfica desde el Mar de Alborán hasta Cataluña, nos sugiere que, efectivamente, ambas son formas de una misma especie, con una ligera tendencia a aumentar el tamaño y a atenuar la coloración a medida que aumenta la profundidad. Además, los escasos ejemplares de coloración uniforme encontrados en aguas profundas son ejemplares subfósiles. Por lo tanto, y atendiendo sólo a las características de la concha, consideramos a *M. coarctata* como sinónimo de *M. costata*.

Mangelia attenuata (Montagu, 1803) (Figs. 50, 51)

Del mismo modo que en el caso anterior, creemos que *M. tenuicostata* (Brugnone, 1868) es sinónimo de *M. attenuata*. Esta especie, que se encuentra desde el litoral hasta los 250 m, disminuye de tamaño al aumentar la profundidad, y atenúa la coloración. Además, las vueltas de espira se van haciendo más escalonadas y las costillas más marcadas, pero la protoconcha no sufre variación alguna. Las Figuras 50 y 51 ilustran la forma de aguas profundas.

Mangelia nuperrima (Tiberi, 1855) (Figs. 52, 53)

Esta especie se diferencia de *Mangelia serga* (Dall, 1881) por poseer vueltas de espira más redondeadas y una boca más ancha. Se ha encontrado un ejemplar fresco en el contenido estomacal de *Astropecten irregularis*, y cuatro conchas en el detrito de "El Parrusset".

Mangelia serga (Dall, 1881) (Figs. 54, 55)

Esta especie se ha citado pocas veces en el Mediterráneo; una vez para Cerdeña (Cecalupo, 1984) y otra vez para el Tirreno Central (Smriglio, Mariottini y Gravina, 1987b). Se ha encontrado un ejemplar con restos de partes blandas en contenidos estomacales de *Astropecten irregularis* y tres conchas en el detrito de "El Parrusset".

Taranis moerchi (Malm, 1861) (Figs. 57, 58, 59)

Esta especie, de concha extremadamente variable, no es rara en el Mediterráneo. Las medidas de la protoconcha ilustrada son las siguientes: 500 mm de

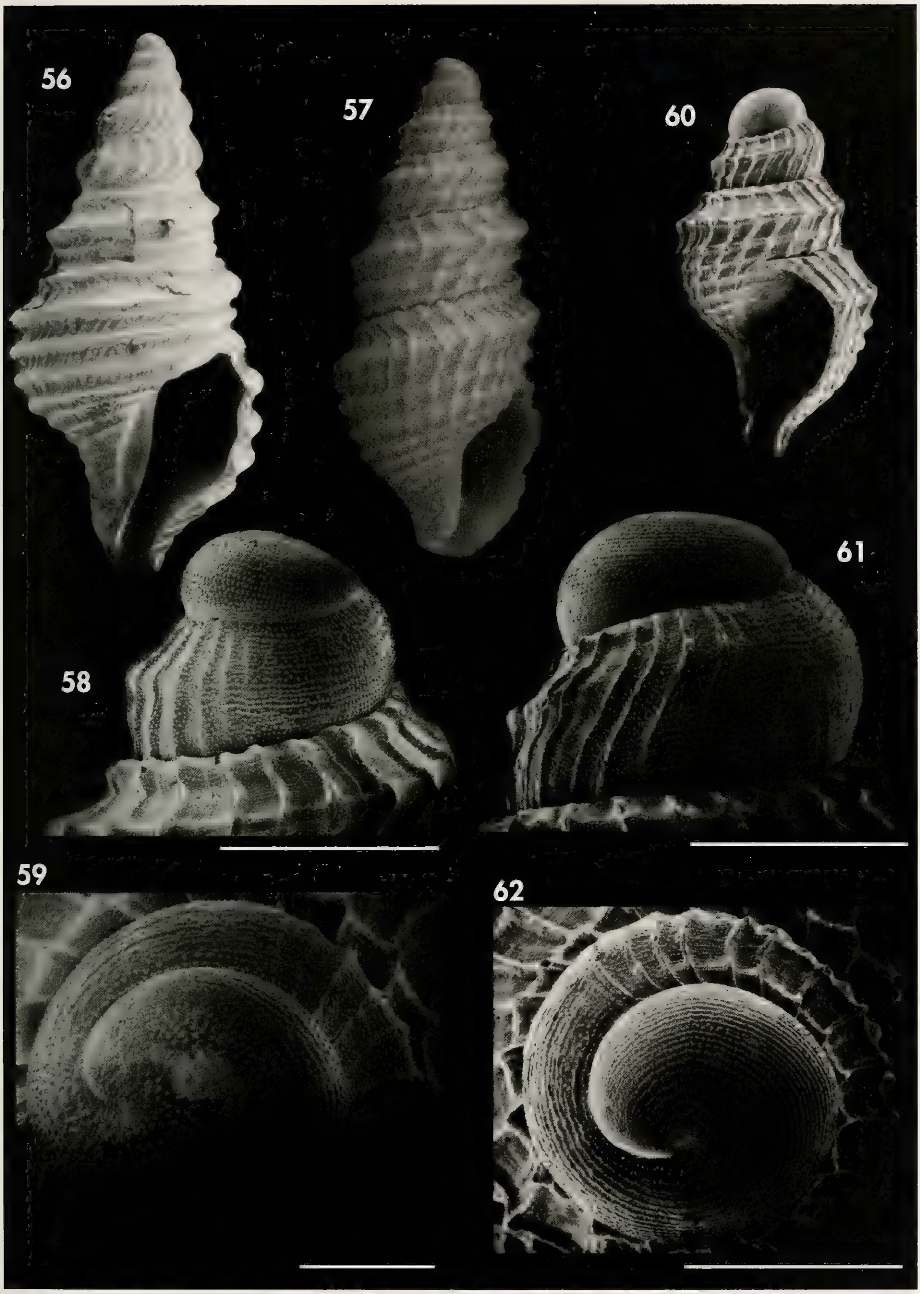


Figura 56. *Microdrillia loprestiana* (EL Parrusset), 3,1 mm. Figuras 57-59 *Taranis moerchi* (El Parrusset). 57: concha de 4,4 mm; 58, 59: protoconcha. Figuras 60-62. *Taranis* sp. (El Parrusset). 60: concha de 2,8 mm; 61, 62: protoconcha. Escalas, 58, 61, 62: 500 µm; 59: 200 µm.
Figure 56. Microdrillia loprestiana *(EL Parrusset), 3.1 mm. Figures 57-59.* Taranis moerchi *(El Parrusset). 57: shell of 4.4 mm; 58, 59: protoconch. Figures 60-62.* Taranis *sp. (El Parrusset). 60: shell of 2.8 mm; 61, 62: protoconch. Scale bars, 58, 61, 62: 500 µm; 59: 200 µm.*

altura y 550 mm de diámetro máximo. Se han encontrado 18 ejemplares (incluyendo juveniles) en el detrito de "El Parrusset".

Taranis sp. (Figs. 60, 61, 62)

Junto a los ejemplares de *T. moerchi*, hemos encontrado una concha de aspecto similar a ésta, pero que difiere en la protoconcha, que es mucho más grande (650 mm de altura y 730 mm de diámetro máximo), y además presenta una escultura puntiforme alineada en cordones desde el mismo ápice de la protoconcha, mientras que en *T. moerchi* los cordones de puntos se desordenan en el ápice. Este ejemplar mide 2, 8 mm de longitud.

Microdrillia loprestiana (Calcara, 1841) (Fig. 56)

Esta especie es común en contenidos estomacales de estrellas a partir de los 60-80 metros, y en el detrito de "El Parrusset".

Pleurotomella demosia (Dautzenber y Fischer, 1896) (Figs. 66, 67, 68)

Nuestros ejemplares se ajustan a la descripción y figuras aportadas por BOUCHET Y WARÉN (1980), aunque el diámetro de la protoconcha es menor. Las medidas que presenta la protoconcha fotografiada (Figs. 67, 68) son las siguientes: 325 mm de diámetro de la P1 y 580 mm de diámetro de la P2.

Esta especie fue citada por primera vez para el Mediterráneo por BOGI (1985), y posteriormente por CECALUPO (1988) para Cerdeña y por BOGI *ET AL.* (1989) para el Tirreno. Hemos encontrado dos ejemplares frescos en contenidos estomacales de *Astropecten irregularis* y dos conchas en el detrito de "El Parrusset".

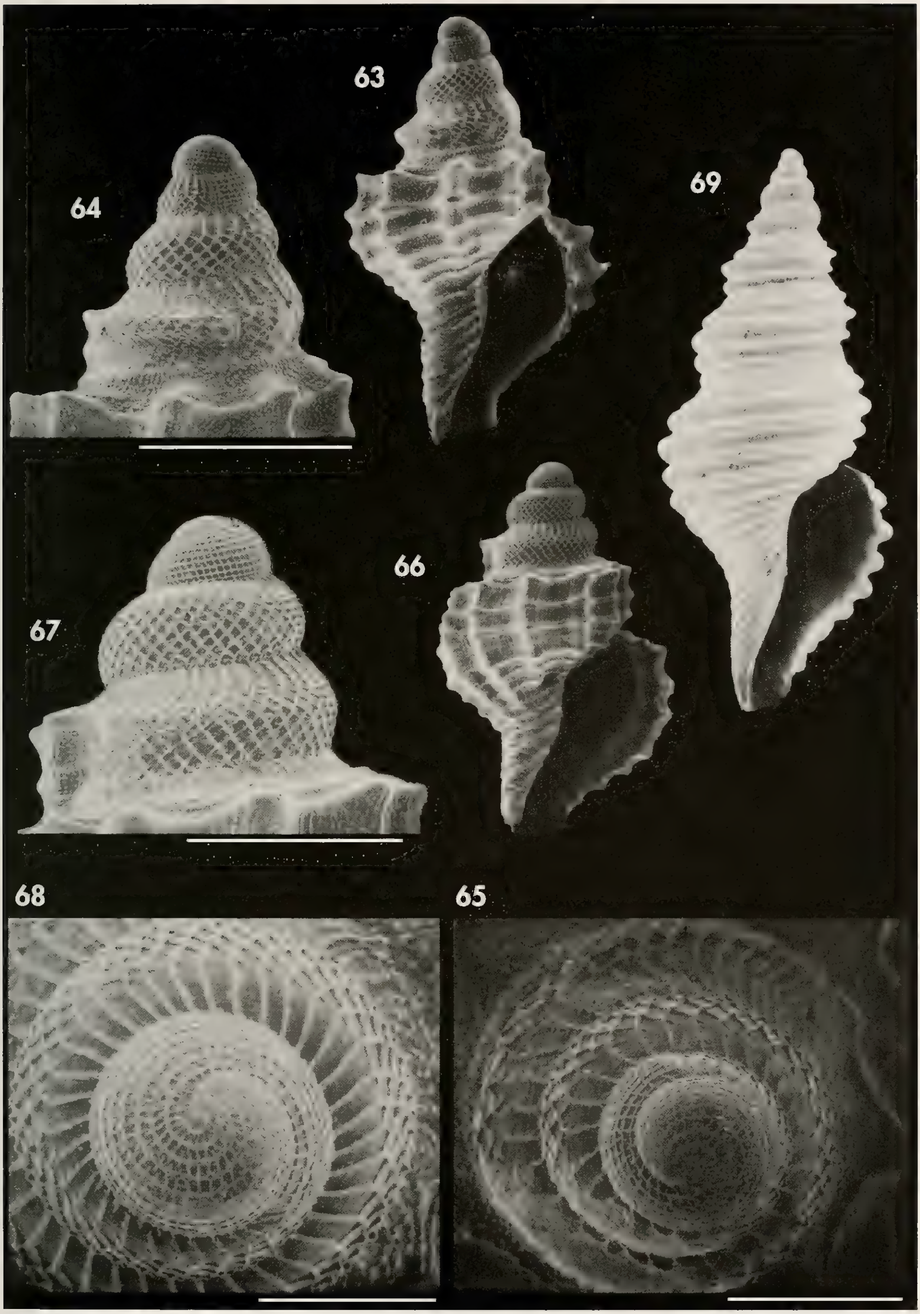
Pleurotomella coeloraphe (Dautzenberg y Fischer, 1896) (Figs. 63, 64, 65)

De esta especie, de aspecto más globoso que *P. eurybrocha* y que *P. demosia*, sólamente se conoce el material de la zona batial de Azores, recolectado en varias estaciones de la expedición MONACO y en una estación de la expedición PORCUPINE (BOUCHET Y WARÉN, 1980). Presenta una protoconcha similar a la de *P. eurybrocha* en cuanto a forma, pero se diferencia en que la protoconcha embrionaria es reticulada (como en *P. demosia*) y no granulada como en *P. eurybrocha*. Las medidas que presenta la protoconcha fotografiada son las siguientes: 210 mm de diámetro de la P1 y 460 mm de diámetro de la P2. El diámetro de la protoconcha a 100 mm del ápice es de 200 mm, al igual que en *P. eurybrocha*.

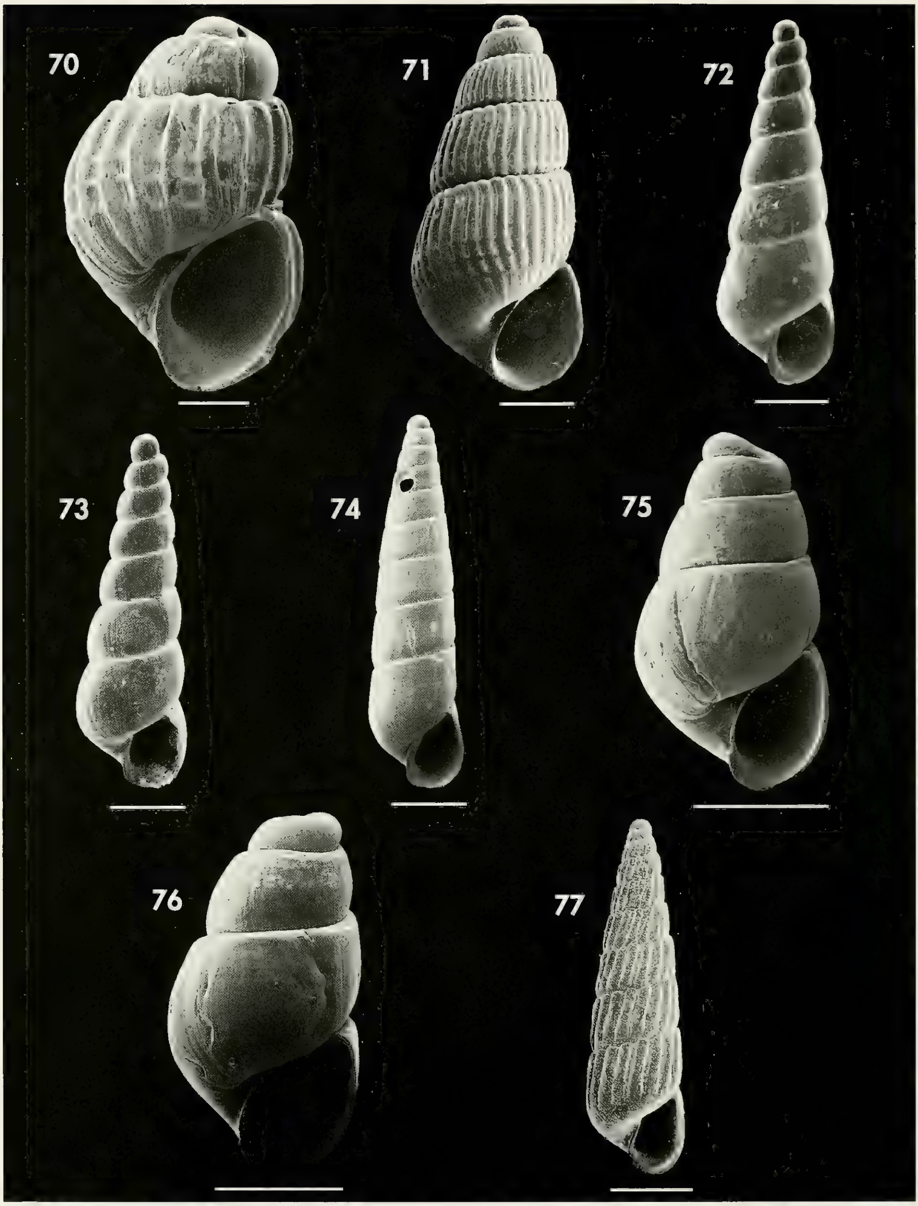
Hemos encontrado 4 ejemplares juveniles en el detrito de "El Parrusset". Se trata por tanto de la primera cita de esta especie para el Mediterráneo.

Familia TJAERNOEIDAE

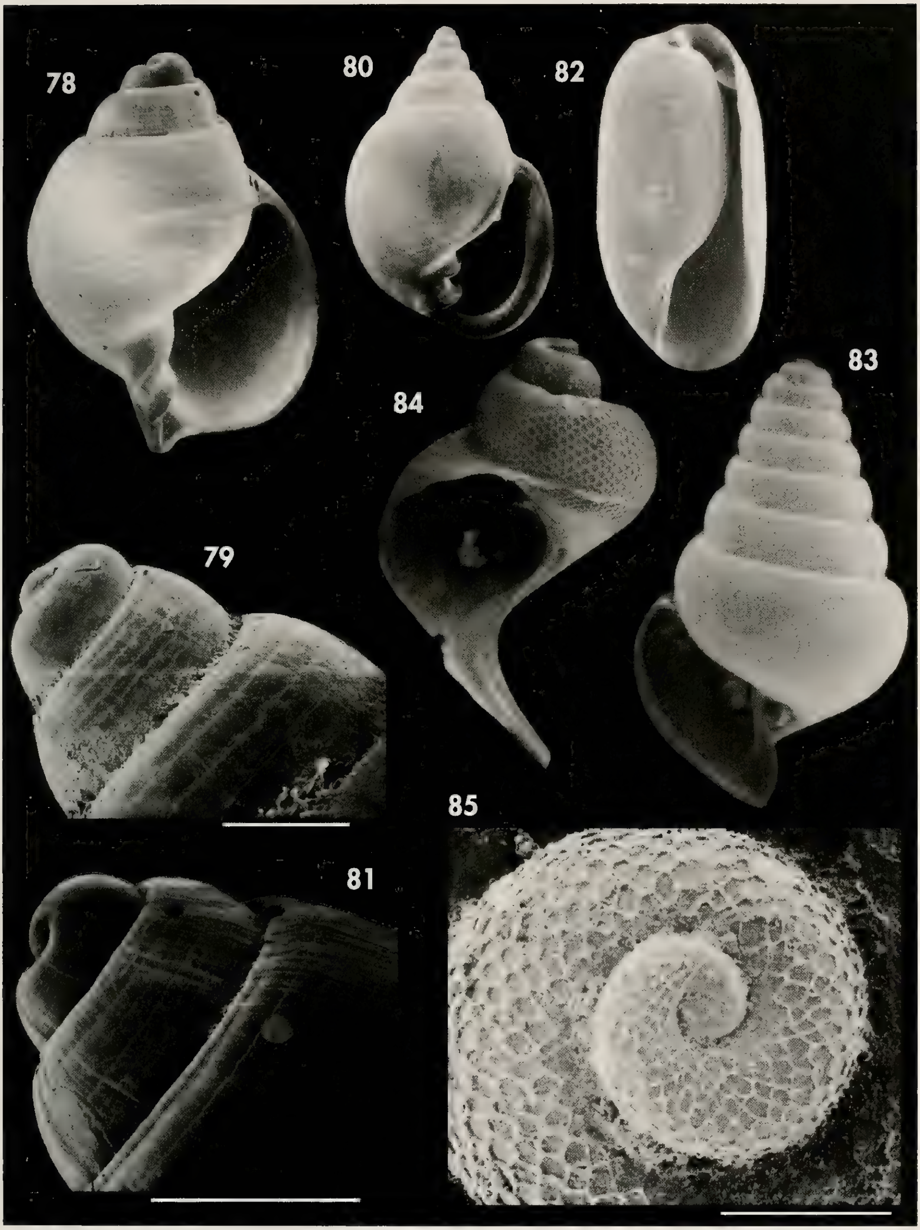
Familia monogenérica de Heterobranchia descrita por WARÉN (1991) en base a la anatomía externa del animal. Previamente, el género *Tjaernoeia*, descrito por WARÉN Y BOUCHET (1988), había sido situado provisionalmente en la familia Pyramidellidae por los mismos autores.



Figuras 63-65. *Pleurotomella coeloraphe* (El Parrusset). 63: juvenil de 1,6 mm; 64, 65: protoconcha. Figuras 66-68. *Pleurotomella demosia* (El Parrusset). 66: juvenil de 2,1 mm; 67, 68: protoconcha. Figura 69. *Teretia teres* (El Parrusset), 4,4 mm. Escalas, 64, 67: 500 µm; 65, 68: 200 µm.
Figures 63-65. Pleurotomella coeloraphe *(El Parrusset). 63: juvenile shell of 1.6 mm; 64, 65: protoconch. Figures 66-68.* Pleurotomella demosia *(El Parrusset). 66: juvenile shell of 2.1 mm; 67, 68: protoconch. Figure 69.* Teretia teres *(El Parrusset), 4.4 mm. Scale bars, 64, 67: 500 µm; 65, 68: 200 µm.*



Figuras 70-77. Familia Pyramidellidae. 70: *Chrysallida brattstroemi* (El Parrusset), 1,1 mm. 71: *Chrysallida dollfusi* (L'Escala, Girona), 2,8 mm. 72: *Eulimella ataktos* (Vilanova), 2,7 mm. 73: *Eulimella ventricosa* (Isla de Alborán), 2,36 mm. 74: *Eulimella unifasciata* (Blanes, Girona), 5,5 mm. 75: *Odostomia afzelii* (Vilanova), 1,5 mm. 76: *Odostomia hansgei* (Vilanova), 1,6 mm. 77: *Turbonilla acutissima* (Mijas, Málaga), 4,4 mm. Escalas, 70: 200 µm; 71, 72, 73, 75, 76: 500 µm; 74, 77: 1 mm.
Figures 70-77. Family Pyramidellidae. 70: Chrysallida brattstroemi *(El Parrusset), 1.1 mm. 71:* Chrysallida dollfusi *(L'Escala, Girona), 2.8 mm. 72:* Eulimella ataktos *(Vilanova), 2.7 mm. 73:* Eulimella ventricosa *(Alborán Island), 2.36 mm. 74:* Eulimella unifasciata *(Blanes, Girona), 5.5 mm. 75:* Odostomia afzelii *(Vilanova), 1.5 mm. 76:* Odostomia hansgei *(Vilanova), 1.6 mm. 77:* Turbonilla acutissima *(Mijas, Málaga), 4.4 mm. Scale bars, 70: 200 µm; 71, 72, 73, 75, 76: 500 µm; 74, 77: 1 mm.*



Figuras 78, 79. *Ringicula* cfr. *leptocheila* (El Parrusset). 78: concha de 2,37 mm; 79: protoconcha. Figuras 80, 81. *Ringicula auriculata* (Vilanova). 80: concha de 3,75 mm; 81: protoconcha. Figura 82. *Cylichnina umbilicata* (Vilanova), 1,3 mm. Figura 83: *Limacina retroversa* (El Parrusset), 2,7 mm. Figuras 84, 85. *Peracle reticulata* (El Parrusset). 84: concha de 2 mm; 85: protoconcha. Escalas, 79, 85: 200 µm; 81: 500 µm.

Figures 78, 79. Ringicula *cfr.* leptocheila *(El Parrusset). 78: shell of 2.37 mm; 79: protoconch. Figures 80, 81.* Ringicula auriculata *(Vilanova). 80: shell of 3.75 mm; 81: protoconch. Figure 82.* Cylichnina umbilicata *(Vilanova), 1.3 mm. Figure 83:* Limacina retroversa *(El Parrusset), 2.7 mm. Figures 84, 85.* Peracle reticulata *(El Parrusset). 84: shell of 2 mm; 85: protoconch. Scale bars, 79, 85: 200 µm; 81: 500 µm.*

Tjaernoeia exquisita (Jeffreys, 1883)

Especie poco frecuente en el Mediterráneo, en donde WARÉN (1991) la señala entre 25 y 200 m. Nosotros hemos encontrado ejemplares a más profundidad en el detrito de "El Parrusset".

Familia ARCHITECTONICIDAE

Basisulcata lepida (Bayer, 1942)

Sólo se han encontrado dos ejemplares vivos en "La Mar de Nit", a unos 40 m de profundidad, en una zona detrítica con grandes colonias de *Bolinus brandaris* (L., 1758), cuyas conchas estaban recubiertas por la anémona *Calliactis parasitica* (Couch).

Familia PYRAMIDELLIDAE (Figs. 70-77)

En el trabajo sobre Pyramidellidae del Mediterráneo español de PEÑAS, TEMPLADO Y MARTÍNEZ (1996) se aporta una gran cantidad de datos sobre la presencia de esta familia en fondos del Garraf. Asimismo, se citaba por primera vez para el Mediterráneo las siguientes especies: *Chrysallida brattstroemi* Warén, 1991, *Eulimella ataktos* Warén, 1991, *Odostomia afzelii* (Warén, 1991), y *Odostomia hansgei* (Warén, 1991), las cuatro comunes en esta zona, y ninguna hallada hasta ahora en ninguna otra localidad del Mediterráneo español. Además, en el mismo trabajo, numerosas especies son citadas por primera vez para el Mediterráneo español, también procedentes del Garraf.

Las especies que no habían sido citadas para el Garraf en el trabajo anterior de PEÑAS *ET AL.* (1996), y que hemos hallado posteriormente, son: *Chrysallida dollfusi* (Kobelt, 1903), *Eulimella unifasciata* (Forbes, 1844), *Eulimella ventricosa* (Forbes, 1844), y *Turbonilla acutissima* Monterosato, 1884.

El hallazgo en "El Parrusset" de una concha subfósil de *Chrysallida pellucida* (Dillwyn, 1817), no contradice la hipótesis de PEÑAS *ET AL.*, (1996), que comentan que, en la actualidad, esta especie atlántica no penetra en el Mediterráneo más allá del mar de Alborán.

Familia SCAPHANDRIDAE

Scaphander punctostriatus (Mighels y Adams, 1841)

Esta especie ha sido citada raras veces en el Mediterráneo (MONTEROSATO, 1880; ROS, 1975; BOUCHET Y TAVIANI, 1989), y ha sido tradicionalmente considerada una especie de aguas profundas del Atlántico. Se han encontrado 6 conchas en el detrito de "El Parrusset".

Familia DISCODORIDIDAE

Taringa faba (Ballesteros, Llera y Ortea, 1984)

Esta especie se encuentra en la playa del búnker de Cubelles, bajo piedras a menos de 50 centímetros de profundidad. Ésta es la localidad tipo de la especie, descrita por BALLESTEROS, LLERA Y ORTEA (1984), donde se puede encontrar con relativa frecuencia.

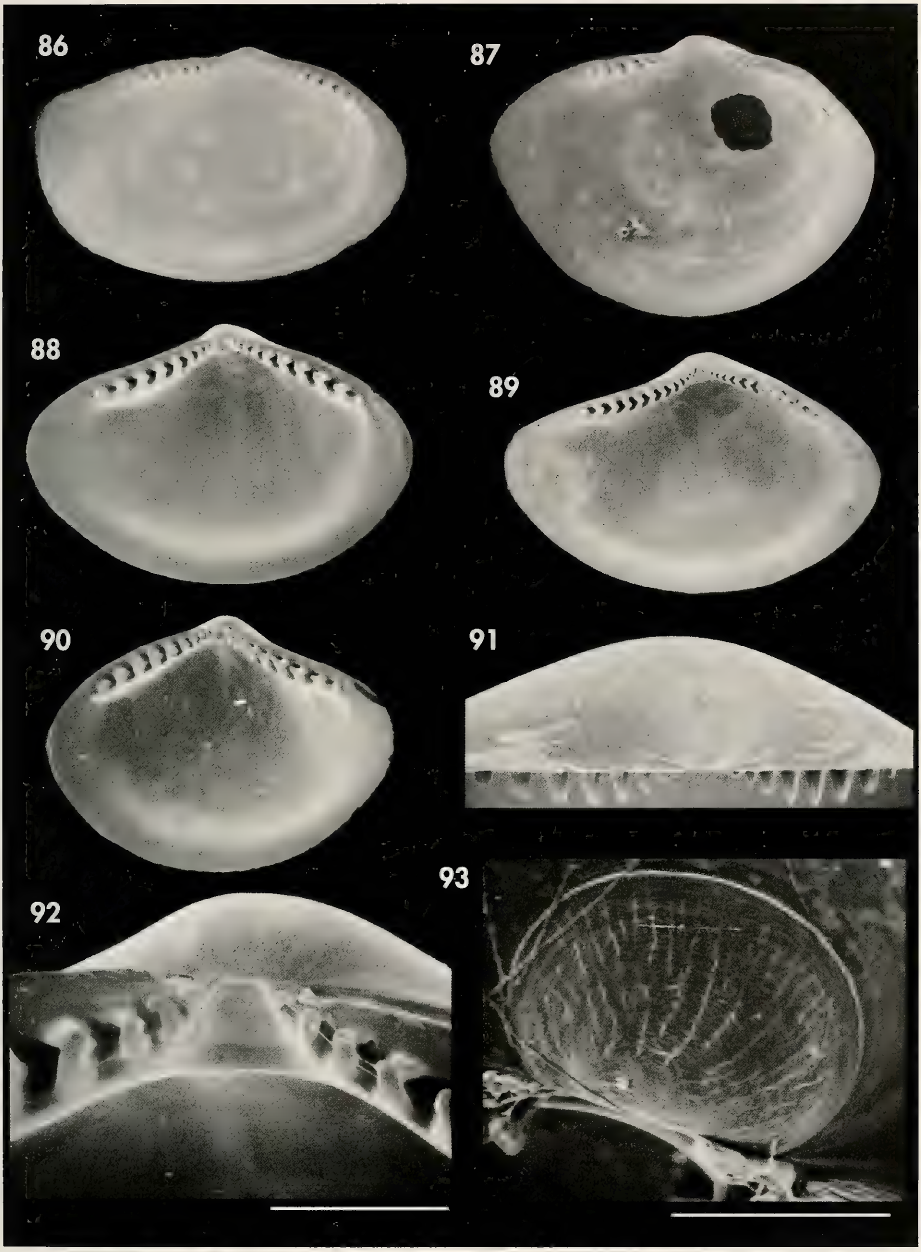


Figura 86. *Yoldiella lucida*, 4,25 mm. Figura 87. *Yoldiella nana*, 2,9 mm. Figuras 88-93. *Yoldiella philippiana*. 88, 89: juveniles de 2,9 y 2,3 mm; 90: adulto de 4,3 mm; 91: juvenil, detalle de los dientes de la charnela; 92: charnela; 93: protoconcha. Todos las especies de El Parrusset, contenido estomacal de *Astropeceten*, 250-350 m. Escalas; 92: 200 µm; 93: 100 µm.
Figure 86. Yoldiella lucida, *4.25 mm. Figure 87.* Yoldiella nana, *2.9 mm. Figures 88-93.* Yoldiella philippiana. *88, 89: juvenile shells of 2.9 and 2.3 mm; 90: adult shell of 4. 3 mm; 91: juvenil shell, hinge lateral view; 92: hinge; 93: protoconch. All the especies from El Parrusset, gut content of* Astropecten, *250-350 m. Scale bars, 92: 200 µm; 93: 100 µm.*

Familia FAVORINIDAE

Favorinus vitreus (Ortea, 1982)

Esta especie fue descrita por ORTEA (1982) en Tenerife (Islas Canarias), a partir de dos ejemplares, y únicamente se ha citado 1 ejemplar para el Mediterráneo, en al Cabo de Palos (Murcia) en rizomas de *Posidonia* a 5 m de profundidad (TEMPLADO, 1982). Se ha recolectado un ejemplar de esta especie en Junio de 1993 en Cubelles, debajo de una piedra a unos 20-30 cm de profundidad.

Clase BIVALVIA

Familia NUCULIDAE

Nucula cfr. *nucleus* (Linnaeus, 1758)

Gofas (*com. pers.*) opina que su presencia en el Mediterráneo es dudosa, siendo *N. hanleyi* Winckworth, 1930, la especie más normal, que presenta un periostraco más brillante, con estrías radiales oscuras, y más alargada anteriormente. SALAS (1996) ilustra un ejemplar de *N. nucleus* del Mediterráneo. Hemos encontrado ejemplares juveniles con una protoconcha que coincide con la descripción de GOFAS Y SALAS (1996), y ejemplares adultos que, aunque han perdido parte del periostraco, asignamos a *N. nucleus.*

Familia YOLDIIDAE

La familia Yoldiidae es la principal familia de Nuculanoidea en el Mediterráneo, y en el Garraf sólo hemos hallado el género *Yoldiella*. Las otras familias de Nuculanoidea no han sido recolectadas en este estudio por presentar una distribución batimétrica de mayor profundidad. Aunque tenemos constancia de la existencia de especies de otras familias en zonas más profundas frente a la costa del Garraf (Dantart, *com. pers.*).

Hemos tratado de recopilar aquí las citas modernas de las especies de la subfamilia Yoldiellinae en el Mediterráneo debido a que la informacion sobre el género es muy dispersa. Sin embargo, no se han tenido en cuenta descripciones originales, citas antiguas ni sinonimias, que se pueden encontrar en los artículos mencionados en esta sección. De todas las citas recopiladas para el Mediterráneo, reconocemos sólo 5 especies. Se han dado entre corchetes los nombres utilizados incorrectamente, o los que han sido considerados como sinonimias.

Yoldiella lucida (Lovén, 1846) (Fig. 86)

Di Geronimo y Panetta (1973): Golfo de Taranto, 940-1000 m
Warén (1989): distribucion Mediterránea entre 100 y 1000 m de profundidad

Es la especie de *Yoldiella* menos frecuente de las halladas en Garraf, habiéndose encontrado sólo tres conchas, dos en contenidos estomacales de estrellas y una en el sedimento, todas del detrito de "El Parrusset", entre 250 y 350 m de profundidad, por lo que se deduce que vive en la zona.

Figura 94. *Bathyarca pectunculoides* (El Parrusset), 1,3 mm. Figura 95. *Bathyarca philippiana* (El Parrusset), 1,3 y 1,6 mm. Figura 96. *Crenella pellucida* (El Parrusset), 710 µm. Figura 97. *Modiolula phaseolina* (El Parrusset), 1,96 mm.

Figure 94. Bathyarca pectunculoides *(El Parrusset), 1.3 mm. Figure 95.* Bathyarca philippiana *(El Parrusset), 1.3 and 1.6 mm. Figure 96.* Crenella pellucida *(El Parrusset), 710 µm. Figure 97.* Modiolula phaseolina *(El Parrusset), 1.96 mm.*

Yoldiella nana (M. Sars, 1865) (Fig. 87)

Cecalupo y Giusti (1986): Isla de Capraia, 400-440 m [*Portlandia frigida* (Torell, 1859)]
Bogi *et al.* (1989): Capo Corso, 150 m [*Portlandia frigida* (Torell, 1859)]
Warén (1989): Banyuls, 650-770 m

Se han encontrado varias conchas en contenidos estomacales de estrellas entre 100 y 350 m de profundidad, y otras en el detrito de "El Parrusset", por lo que se deduce que también vive en la zona.

Yoldiella philippiana (Nyst, 1845) (Figs. 88-93)

Di Geronimo y Panetta (1973): Golfo de Taranto, 350-1000 m [*Yoldiella tenuis* (Philippi)]
Di Geronimo (1974): Jónico [*Yoldiella tenuis* (Philippi)]
Cecalupo y Giusti (1986): varios ejemplares vivos, Isla de Capraia, 400-440 m
Warén (1989): Mediterráneo, 100-300 m
Bonfitto y Sabelli (1995): Cerdeña, 245-1707 m

Es la especie más abundante, apareciendo tanto en sedimentos como en contenidos intestinales de *Astropecten*, desde los 60 hasta los 350 m de profundidad. Se han encontrado numerosos juveniles vivos.

Las otras dos especies mediterráneas de este género, *Yoldiella messanensis* (Seguenza, MS, Jeffreys, 1870) y *Yoldiella seguenzae* Bonfitto y Sabelli, 1995, no se han encontrado en la zona de estudio. La primera ha sido citada en el Mediterráneo en general (150-3000 m) y en el mar de Alborán (60-1235 m) por TERRENI (1980), CECALUPO Y GIUSTI (1986), WARÉN (1978, 1989), ALLEN Y HANNAH (1989) y SALAS (1996). La segunda sólo se conoce de Cerdeña (245-1707 m) y mar de Alborán, entre 480 y 1005 m (BONFITTO Y SABELLI, 1995; SALAS 1996).

Familia MYTILIDAE

El género *Idas* en el Mediterráneo está representado por tres especies (WARÉN, 1991), asociadas siempre a restos de esqueletos de cetáceos. Además de este hábitat, *I. argenteus* Jeffreys, 1876 e *I. ghisotti* Warén y Carozza, 1990 también pueden encontrarse en restos de troncos (WARÉN, 1991, 1993). La utilización del género *Idas* Jeffreys, 1878, en vez de *Idasola* Iredale, 1915, contrariamente a lo propuesto por DELL (1987), se basa en lo expuesto por WARÉN (1991).

Idas cfr *ghisottii* Warén y Carrozza, 1990

En un tronco de madera arrojado a la playa tras una tormenta, se ha encontrado un ejemplar que asignamos a esta especie, junto con varios ejemplares de Teredinidae. Esta especie sólo se ha encontrado asociada a restos de madera en el Mediterráneo por CARROZZA (1984), que la identificó erróneamente como *Myrina modiolaeformis* Sturany, 1896. Fue corregido posteriormente por WARÉN Y CARROZZA (1990), que la describieron como nueva especie. De todas formas, y debido a la pérdida del único ejemplar hallado, la asignación de este especimen podría ser errónea, aunque estamos seguros de que no se trata de *I. simpsoni* (Marshall, 1900).

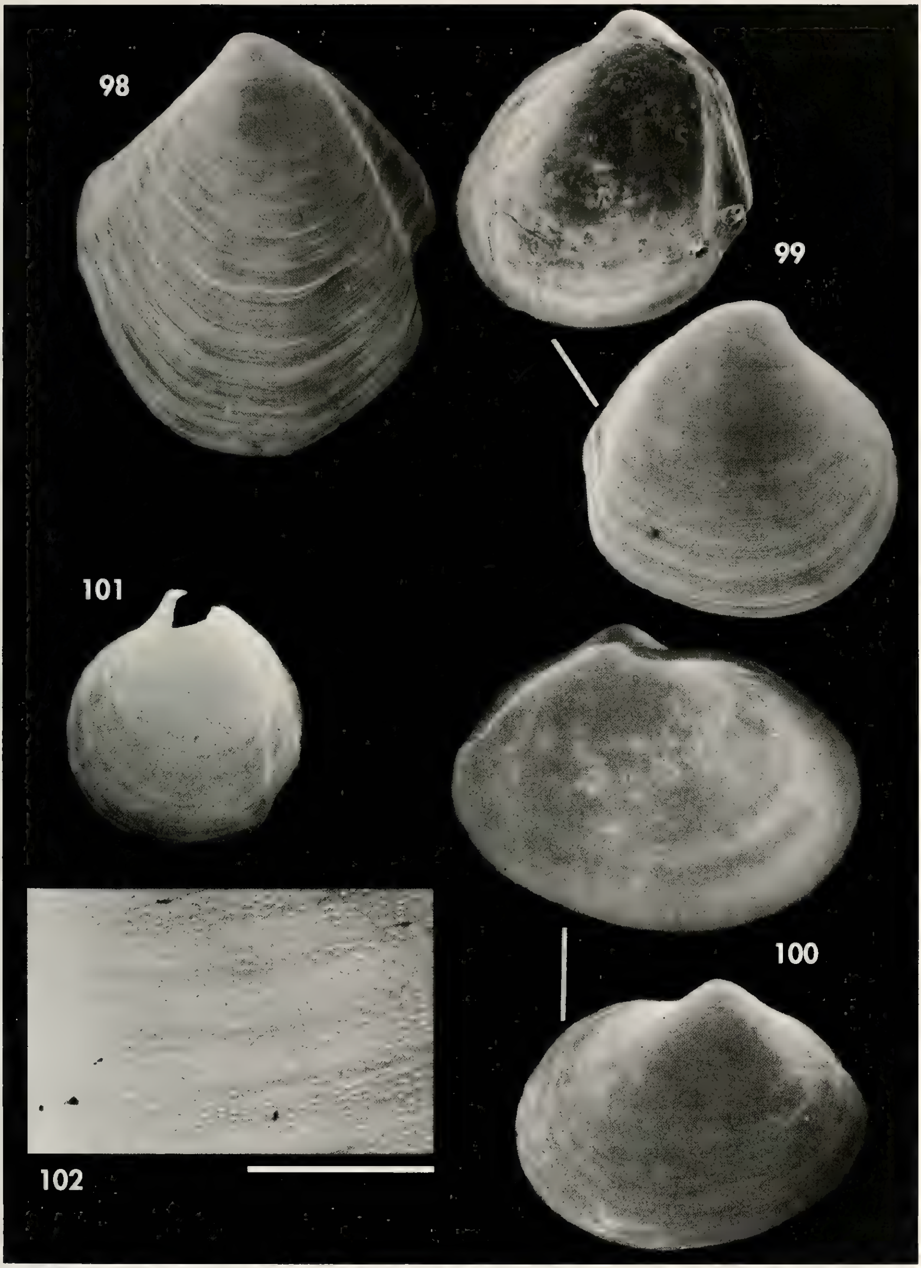


Figura 98. *Thyasira (T.) biplicata* (El Parrusset), 4,9 mm. Figura 99. *Thyasira (T.) obsoleta* (El Parrusset), 1,46 y 1,87 mm. Figura 100. *Thyasira (P.) subovata* (El Parrusset), 1 y 1,16 mm. Figuras 101, 102. *Thyasira (Parathyasira) granulosa.* 101: ejemplar de 5.4 mm. 102: detalle de la granulación de la concha. Escala 400 µm.

Figure 98. Thyasira (T.) biplicata *(El Parrusset), 4.9 mm. Figure 99.* Thyasira (T.) obsoleta *(El Parrusset), 1.46 and 1.87 mm. Figure 100.* Thyasira (P.) subovata *(El Parrusset), 1 and 1.16 mm. Figures 101, 102.* Thyasira (Parathyasira) granulosa. *101: shell of 5.4 mm. 102: shell granulation detail. Scale bar 400 µm.*

Idas simpsoni (Marshall, 1900)

Se trata de otro Mytilidae interesante, que vive en restos orgánicos de esqueletos de cetáceos o peces, aunque mucho más común que el anterior y de distribución más amplia. Se han encontrado varios ejemplares asociados a esqueletos.

Modiolula phaseolina (Philippi, 1844) (Fig. 97)

Se han encontrado unos pocos ejemplares vivos en el detrito de "El Parrusset", aunque esta especie destaca por la gran cantidad de conchas Würmienses de gran tamano (más de 20 mm) encontradas en esta localidad.

Familia PECTINIDAE

Hemos incluido en esta familia las especies clasificadas por algunos autores como Propeamussiidae (o Amussiidae). De todas formas, esta clasificación es provisional hasta que se realice un estudio filogenético que resuelva la cuestión. Hemos seguido la sistemática utilizada por WAGNER (1991), excepto en la separación de Pectinidae y Amussiidae. Para algunas especies de "Amussiidae", hemos seguido a SMRIGLIO Y MARIOTTINI (1990).

Pseudamussium septemradiatum (O. F. Müller, 1776)

Se han encontrado ejemplares vivos de esta especie en fondos de fango entre 150 y 200 m de profundidad, mientras que VINYAS (1981) la consideraba como una especie de aguas frías, que supuestamente se había extinguido del Mediterráneo, aunque abundante en los sedimentos Würmienses (MARS, 1958; MARTINELL Y JULIÀ-BRUGUES, 1973; VINYAS, 1981; DOMÈNECH Y MARTINELL, 1982). SALAS (1996) la cita viva para el mar de Alborán.

Flexopecten glaber (Linnaeus, 1758)

Gofas (*com. pers.*) ha comentado que se trata de una especie más bien lagunar, rara en el Mediterráneo occidental, y que algunos juveniles grandes de *F. flexuosus*, que no presentan aún la flexuosidad típica de la especie, pueden ser confundidos con *F. glaber*. Hemos encontrado una única valva de esta especie, de 35 mm de altura con 10 costillas principales, claramente diferente de *F. flexuosus*, cuyos mayores ejemplares encontrados en la zona miden 28 mm y presenta 5 costillas principales.

Familia LIMIDAE

Limatula cfr. *gwyni* (Sykes, 1903)

Se ha encontrado una única valva fresca procedente del detrito de "El Parrusset". El ejemplar se destruyó durante el proceso de montaje para el M.E.B. El color era blanco y presentaba una forma y tamaño similar a *L. subovata*, aunque totalmente lisa y sin restos de costillas radiales.

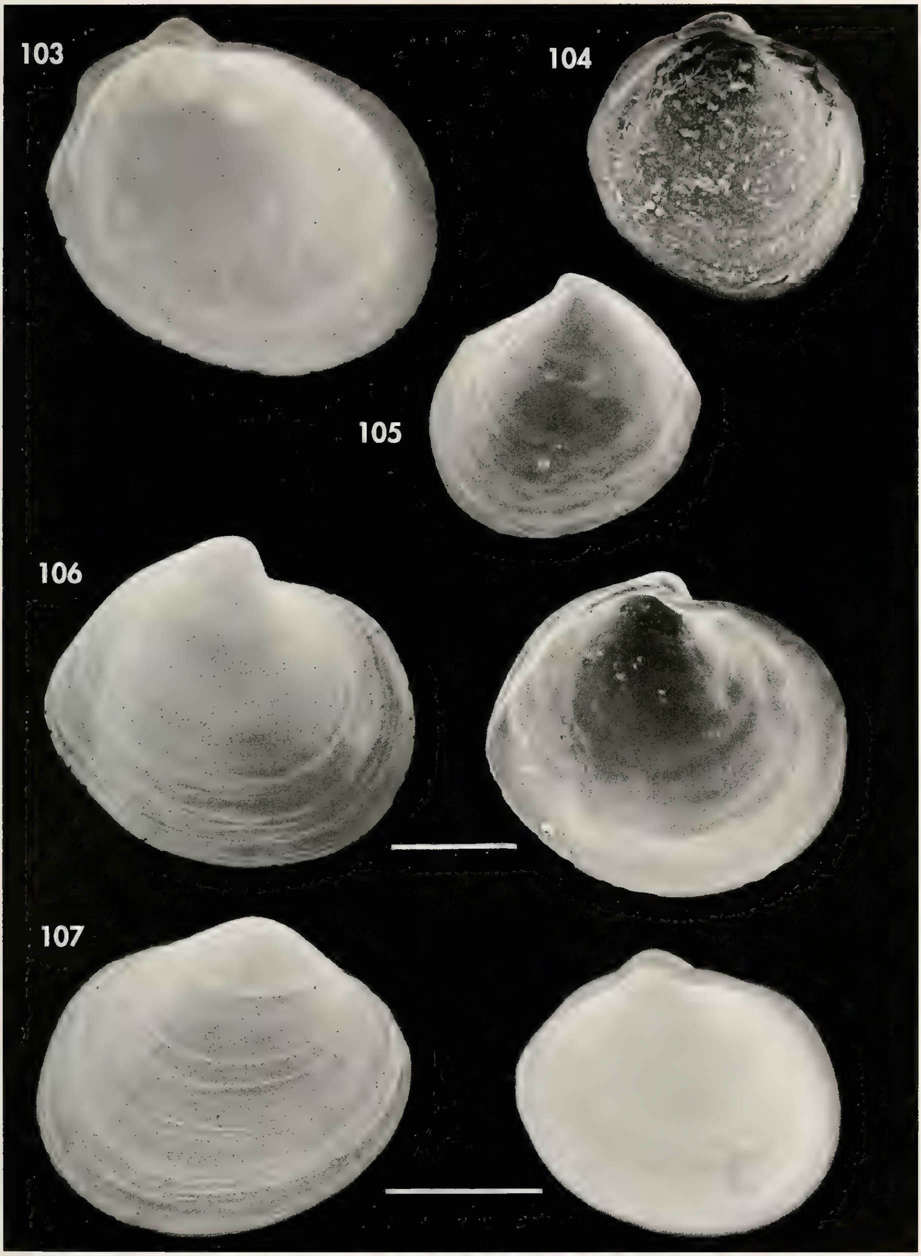


Figura 103. *Thyasira (Leptaxinus) incrassata* (El Parrusset), 1,66 mm. Figura 104. *Thyasira (Axinulus) croulinensis* (El Parrusset), 1,26 mm. Figura 105. *Thyasira (A.) eumyaria* (El Parrusset), 2,9 mm. Figura 106. *Thyasira (Mendicula) ferruginea* (El Parrusset), 1,46 mm. Figura 107. *Arculus* sp. (El Parrusset), 1,02 mm y 1,16 mm.

Figure 103. Thyasira (Leptaxinus) incrassata *(El Parrusset), 1.66 mm. Figure 104.* Thyasira (Axinulus) croulinensis *(El Parrusset), 1.26 mm. Figure 105.* Thyasira (A.) eumyaria *(El Parrusset), 2.9 mm. Figure 106.* Thyasira (Mendicula) ferruginea *(El Parrusset), 1.46 mm. Figure 107.* Arculus *sp. (El Parrusset), 1.02 mm and 1.16 mm.*

Familia LUCINIDAE

Lucinoma borealis (Linnaeus, 1767)

Se han encontrado ejemplares vivos de gran tamaño (hasta 47,9 mm, un ejemplar de la coleccion de J. L. Ferrer), en fondos de fango entre 60 y 80 m de profundidad.

Familia THYASIRIDAE (Figs. 98-106)

Los tiasíridos son la principal familia de bivalvos que habita en el talud. Muchas especies viven desde el circalitoral hasta profundidades abisales. Las especies atlánticas han sido recientemente revisadas a nivel morfológico por PAYNE Y ALLEN (1991), pero son pocos los trabajos sobre este grupo en el Mediterráneo. La descripción de una nueva especie mediterránea por CARROZZA (1981), así como las redescripciones de algunas especies de Monterosato publicadas por GAGLINI (1991) son las obras modernas más importantes para este mar. Además, existen algunas citas dispersas (p. e. DI GERONIMO Y PANETTA, 1973; TERRENI, 1980; CARROZZA, 1984; CIANFANELLI Y TALENTI, 1987; CECALUPO Y GIUSTI, 1989), pero no hay ningún trabajo taxonómico de revisión importante. Tampoco pretendemos aquí realizar una revisión taxonómica del grupo, pero hemos querido fotografiar las 8 especies aparecidas en el detrito de "El Parrusset" (Figs. 98-106), constituyendo 6 de ellas la primera cita para el Mediterráneo español.

Thyasira biplicata (Philippi, 1836) (Fig. 98)

Esta especie, fue descrita por PHILIPPI (1836) para zonas abisales del Mar Mediterráneo, pero ha sido referida en la literatura como *T. flexuosa* (Montagu, 1803), que es una especie litoral atlántica con la ondulación posterior más suave (Gofas, *com. pers.*), de presencia dudosa en el Mediterráneo.

Familia MONTACUTIDAE

Epilepton clarkiae (Clark, 1852)

Todos los ejemplares se han encontrado en una comunidad dominada por *Turritella communis* Risso, 1826, a unos 60 m de profundidad.

Epilepton sp.

Este pequeño *Epilepton*, aparecido en el detrito coralígeno de "El Parrusset" está en este momento en proceso de descripción.

Familia NEOLEPTONIDAE

Arculus sp. (Fig. 107)

Hemos identificado provisionalmente estos ejemplares, hallados también en "El Parrusset", dentro del género *Arculus*.

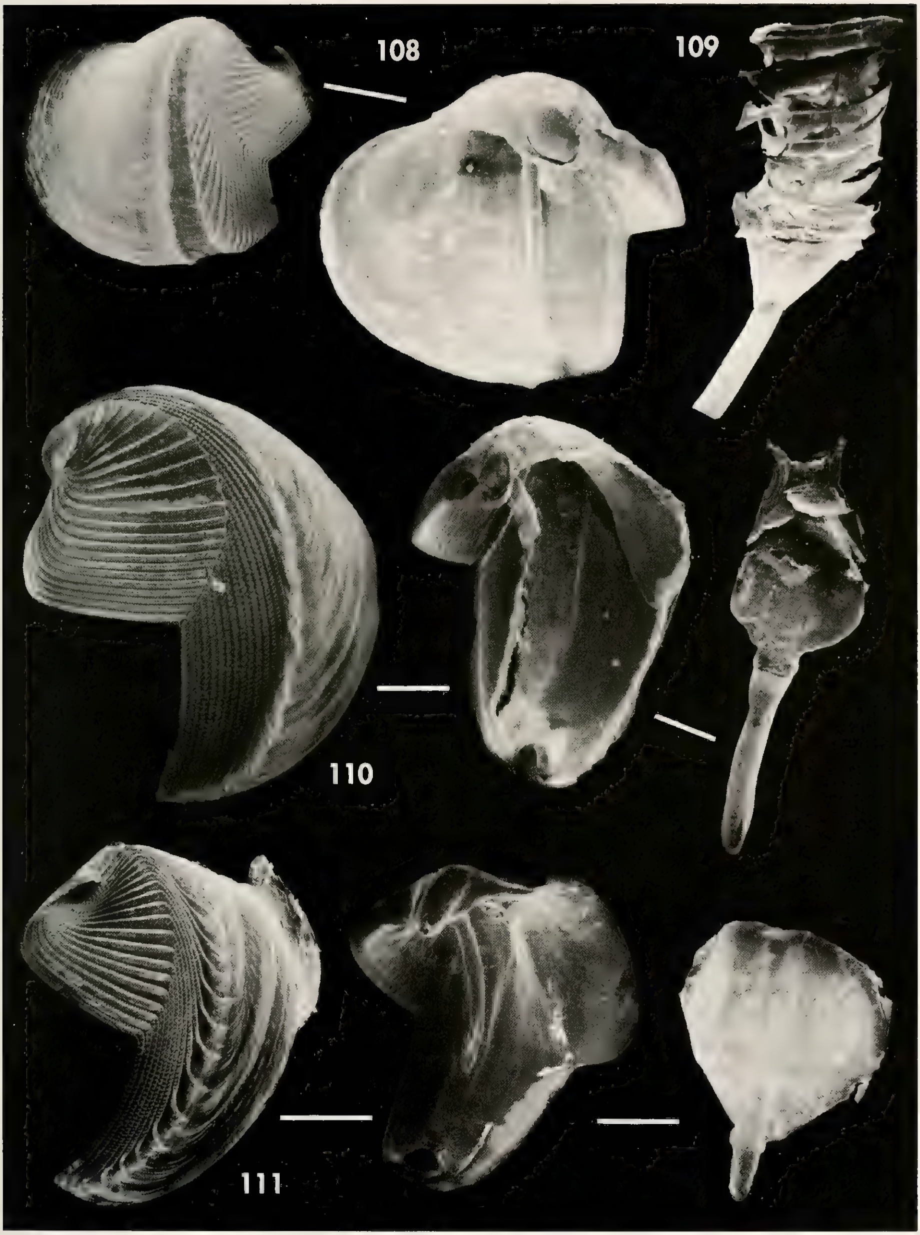


Figura 108. *Xylophaga dorsalis* (Vilanova): exterior valva derecha, 3,4 mm; interior valva izquierda, 1,6 mm. Figura 109. paleta de *Bankia carinata* (Vilanova), 4,7 mm. Figura 110. *Lyrodus pedicellatus* (Vilanova): exterior valva izquierda, 1,9 mm; interior valva derecha, 2,16 mm; paleta de 2,5 mm. Figura 111. *Nototeredo norvegica* (Vilanova): exterior valva izquierda, 1, 38 mm; interior valva derecha, 1,5 mm; paleta de 1,7 mm.

Figures 108. Xylophaga dorsalis *(Vilanova): outside of right valve, 3.4 mm; inside of left valve, 1.6 mm. Figure 109. pallet of* Bankia carinata *(Vilanova), 4.7 mm. Figures 110.* Lyrodus pedicellatus *(Vilanova): outside of left valve, 1.9 mm; inside of right valve, 2.16 mm; pallet of 2.5 mm. Figure 111.* Nototeredo norvegica *(Vilanova): outside of left valve, 1.38 mm; inside of right valve, 1.5 mm; pallet of 1.7 mm.*

Familia ASTARTIDAE

Goodallia sp.

En el detrito de "El Parrusset" han aparecido ejemplares pertenecientes al género *Goodallia*, similares al taxon *G. macandrewi* Smith, 1881, que posiblemente se trate de una nueva especie.

LOS MOLUSCOS DE "EL PARRUSSET": Como se comentaba anteriormente, "El Parrusset" es una biocenosis de coral blanco (PÉRÈS Y PICARD, 1964) con fango, cuyas especies predominantes son los madreporarios *Dendrophyllia cornigera* (Lamarck) y *Caryophyllia* sp., asociada a una tanatocenosis del Würmiense, con la presencia de algunas especies subfósiles que actualmente están extintas en el Mediterráneo. En esta localidad se han obtenido numerosas especies de moluscos de profundidad, siendo *Trophon barvicensis* y *Pleurotomella coeloraphe* la primera vez que se citan para el Mediterráneo, y otras la primera vez que se citan para el litoral Mediterráneo español.

Una comunidad muy similar a la de "El Parrusset" ha sido descrita por SMRIGLIO, MARIOTTINI Y GRAVINA (1987a; 1987b) para el mar Tirreno Central, donde estudiaron una biocenosis de coral blanco con detrito fangoso situada entre 400 y 600 m de profundidad, en la que la especie de madreporario predominante es *Dendrophyllia cornigera* (Lamarck). Aunque se trate de dos comunidades muy parecidas desde un punto de vista biológico y paleontológico, las especies de moluscos que se encuentran en la localidad del Tirreno Central (SMRIGLIO *ET AL*., 1987a; 1987b; 1988a; 1988b; 1989; 1993) son características de aguas más profundas. Sin embargo, algunas de las especies son coincidentes en ambas biocenosis, como por ejemplo *Microdrillia lopestriana* (Calcara, 1841), *Mangelia serga* (Dall, 1881) y *Teretia teres* (Forbes, 1844), entre los túrridos.

En cuanto a los bivalvos actuales encontrados en esta biocenosis, los grupos mayoritarios son Nuculidae, Yoldiellidae, *Bathyarca*, *Astarte*, Veneridae, Thyasiridae, Pectinidae y *Xylophaga*, siendo *Kelliella abyssicola* (Forbes, 1844) la especie viva más abundante, tanto en detritos como en contenidos estomacales de estrellas. ALLEN (1979) en un trabajo sobre bivalvos abisales Atlánticos, comenta que el 95% de especies de bivalvos de sustratos blandos son Protobranchia, Septibranchia y Thyasiridae, mientras que para sustratos duros, predominan las especies con biso, como *Bathyarca*, *Limopsis* y *Dacrydium*. Además, encuentra especies pequeñas, generalmente menores de 5 mm. En este trabajo se han encontrado prácticamente los mismos grupos, aunque representados por especies o géneros de menor profundidad y por norma general, de tallas mayores.

El primer yacimiento Würmiense conocido para el litoral catalán fue el Cap de Creus (Girona), descrito por PRUVOT Y ROBERT (1897), posteriormente estudiado por MARS (1958). Otro yacimiento situado en el Cap de Begur (Girona) ha sido descrito por MARTINELL Y JULIÀ-BRUGUES (1973). Trabajos posteriores sobre estos yacimientos Würmienses de la costa de Girona son, entre otros, los de VINYAS (1981) y DOMÈNECH Y MARTINELL (1982). En cuanto a los fondos blandos del litoral catalán, la primera fauna malacológica Würmiense fue descrita por MARTINELL, DOMÈNECH Y DE VILLALTA (1986) para el delta del Ebro (Tarragona).

La tanatocenosis Würmiense que aquí se describe es el origen de algunas de las especies subfósiles que se encuentran en el área. Éste es el caso de los Gasterópodos: *Iothia fulva* (O. F. Müller, 1776), *Calliostoma zizyphinum* (Linnaeus, 1758), *Danilia otaviana* (Cantraine, 1835), *Capulus ungaricus* (Linnaeus, 1758), *Trivia multilirata* (Sowerby, 1870), *Erato voluta* (Montagu, 1803), *Ranella olearia* (Linnaeus,

1758), *Buccinum undatum* Linnaeus, 1758, *Neptunea contraria* (Linnaeus, 1771), y *Murexul aradasi* (Poirier, 1883 ex Monterosato ms.), que se encuentran sólo como especies subfósiles en el área de estudio. Entre los Bivalvos, destacan los grandes ejemplares de *Modiolula phaseolina* (Philippi, 1844), *Chlamys islandica* (O. F. Müller, 1776), *Pseudamussium septemradiatum* (O. F. Müller, 1776), *Arctica islandica* (Linnaeus, 1767), *Glossus humanus* (Linnaeus, 1758), *Globivenus effosa* (Bivona, 1836), *Gouldia minima* (Montagu, 1803), *Pitar mediterranea* Tiberi, 1855, *Venus casina* Linnaeus, 1758 y *Panopea norvegica* (Spengler, 1793). Al contrario que los Gasterópodos, muchas de estas especies también se encuentran vivas a menos profundidad, o incluso en el mismo sedimento, como es el caso de *M. phaseolina*. Las especies de Bivalvos que se encuentran en forma subfósil exclusivamente son *C. islandica*, *A. islandica*, y *P. norvegica*, especies de aguas frías que se han extinguido del Mediterráneo (VINYAS, 1981), y *G. effosa*, que vive en zonas profundas del Mediterráneo (Mar de Alborán).

La malacofauna del sedimento Würmiense de fondos blandos que aquí señalamos, tiene una composición similar a la de los yacimientos de la costa de Girona descritos por los autores mencionados más arriba. De todas formas, la mayoría de los trabajos anteriores están únicamente basados en especies grandes debido a la metodología de muestreo empleada (Martinell, *com. pers.*). En los moluscos de "El Parrusset" destaca la ausencia de *Buccinum humphreysianum* Bennet, 1824 (aunque se han encontrado conchas en otras zonas del Garraf), y de *Modiolus modiolus* (Linnaeus, 1758), presentes en casi todos los otros yacimientos de la costa catalana, así como la ausencia de *Colus islandicus* (Gmelin, 1791), abundante en los yacimientos de la costa de Girona.

CONTENIDOS ESTOMACALES DE *ASTROPECTEN*: Los contenidos estomacales de Equinodermos y otros depredadores han sido investigados por diversos malacólogos, como método sencillo para recolectar numerosas especies, principalmente micromoluscos de profundidad. Trabajos científicos de este tipo han sido realizados en el Mediterráneo español, concretamente en las islas Baleares (GASULL Y CUERDA, 1974) y en la bahía de Almería (SIERRA, GARCÍA Y LLORIS, 1978), así como en la costa atlántica española, en la Ría de Ares (Galicia) (CRISTOBO-RODRÍGUEZ, TRONCOSO, URGORRI-CARRASCO Y RÍOS-LÓPEZ, 1988), entre otros.

En este trabajo, el número de especies de Moluscos encontradas en los contenidos estomacales de *Astropecten* spp. es de 118: 1 Poliplacóforo, 90 Gasterópodos, 25 Bivalvos y 2 Escafópodos). Si bien no se ha recopilado información cuantitativa en los muestreos, sí se tienen datos cualitativos, de los que se ha podido extraer la siguiente información:

- En el Garraf *A. aranciacus* es más común entre los 40 y los 80 m de profundidad en fondos fangosos, mientras que *A. irregularis* es abundante en un rango batimétrico mucho más amplio y en todo tipo de fondos. Casi todas las especies halladas en *A. aranciacus* se encuentran en *A. irregularis*, aunque en esta última se trata de individuos más pequeños o juveniles.
- El Gasterópodo predominante en todas las profundidades estudiadas fue *Alvania testae* (Aradas y Maggiore, 1843), representando aproximadamente el 50% de individuos encontrados.
- El Bivalvo predominante hasta los 80 m fue *Timoclea ovata* (Pennant, 1777), y a partir de esta profundidad predominó *Kelliella abyssicola* (Forbes, 1844).
- En "El Parrusset", existe una relación directa entre el número de ejemplares vivos de Nuculidae, Nuculanidae y Yoldiidae encontrados en los contenidos estomacales y los hallados en el sedimento, pero ésto no ocurre en el resto de grupos estudiados.
- En general, se observó una reducción del tamaño de muchas especies (sobre todo apreciable en grupos abundantes, como Pyramidellidae) a medida que aumentó la profundidad. Este hecho ha sido comentado por ALLEN (1979), que encuentra una disminución de las tasas de crecimiento relacionada con el incremento de la profundidad.

NUEVAS CITAS PARA EL MEDITERRÁNEO ESPAÑOL: Como se señaló anteriormente, en la lista de especies se identifican con un asterisco aquellas que, de acuerdo con la bibliografía, se citan por primera vez en el litoral Mediterráneo español, y con dos asteriscos las que se citan por primera vez para el Meditérraneo en general. En este apartado no se han tenido en cuenta las citas del estrecho de Gibraltar como pertenecientes al Mediterráneo.

La publicación del catálogo provisional no crítico de los Bivalvos del Mediterráneo español de BONNIN Y RODRÍGUEZ-BABÍO (1990), basado en la bibliografía, nos ha facilitado el trabajo de recopilación de citas. En cuanto a los Gasterópodos, no existe ningún catálogo actualizado, exceptuando algunas monografías de varios grupos, como Cocculiniformia (DANTART Y LUQUE, 1994); Pyramidellidae (PEÑAS *ET AL.*, 1996); Opistobranchia (CERVERA, TEMPLADO, GARCÍA-GÓMEZ, BALLESTEROS, ORTEA, GARCÍA, ROS, Y LUQUE, 1988); o el género *Mitrella* (LUQUE, 1986). Por ello, la constatación de nuevas citas se hace dificultosa y requiere la consulta de numerosos trabajos muy dispersos.

En total se reportan 53 nuevas citas para el Mediterráneo español, siendo la mención de *Trophon barvicensis* y *Pleurotomella coeloraphe* las primeras citas para el Mediterráneo en general.

CONCLUSIONES

Este estudio confirma la presencia en el Garraf de gran parte de la malacofauna típica del Mediterráneo español (exceptuando la zona de Alborán). Sin embargo, se ha constatado la ausencia de algunas especies consideradas comunes en áreas cercanas como *Scissurella costata* d'Orbigny, 1824, *Sinezona cingulata* (O. G. Costa, 1861), *Gibbula ardens* (von Salis, 1793), *G. adansonii* (Payraudeau, 1826), *G. rarilineata* (Michaud, 1829), *G. umbilicaris* (Linnaeus, 1758), *Jujubinus gravinae* (Dautzenberg, 1881), *Rissoa variabilis* (von Mühlfeldt, 1824), *Alvania mamillata* Risso, 1826, o *Mitrella gervillei* (Payraudeau, 1826), o por ejemplo, la presencia de sólo 2 skenéidos pertenecientes a dos especies diferentes, y que no se haya encontrado ningún ejemplar de esta familia en fondos de maërl, en los que son comunes en otras localidades.

Finalmente, podemos concluir que la comarca del Garraf es una zona rica en moluscos marinos debido a las particularidades de sus fondos. Prueba de ello son las 53 nuevas citas para el Mediterráneo español. Muchas de estas especies viven probablemente en otras zonas de nuestras costas, pero, debido a su pequeño tamaño, podrían haber pasado desapercibidas. Los autores consideran que la prospección con medios adecuados de las zonas más profundas de esta comarca podría contribuir a ampliar el conocimiento de la malacofauna del litoral español, y que sería interesante recolectar vivas algunas de las especies que aquí se han encontrado, de las que no se conoce el animal.

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Scaphopoda from the Spanish coasts

Escafópodos de las costas españolas

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ABSTRACT

The scaphopod molluscs collected at 29 stations of the Fauna Iberica projects I - III along the entire Spanish mainland coast and the Balearic Islands belong to 12 species from 7 genera and 5 families. These species are listed together with their synonyms, original descriptions, and geographic and bathymetric ranges in this material and from the literature. None of the species are found to extend either range in these samples. On the other hand, some otherwise common scaphopods are not represented. Some of the species have extensive fossil records, and in *Entalina tetragona* and *Antalis inaequicostata*, problems of synonymy and historical biogeography are discussed.

RESUMEN

En el presente trabajo se relacionan aquellas especies de escafópodos encontradas en 29 estaciones de las costas españolas de la península Ibérica y de las islas Baleares durante las campañas FAUNA I-III. En total se han hallado 12 especies pertenecientes a 7 géneros y 5 familias. Para cada especie se proporciona una lista de sinónimos, la descripción original y los rangos de distribución geográfica y batimétrica, obtenidos a partir de este material y de la bibliografía. Los datos que proporcionan estas muestras no permiten extender rangos de distribución de ninguna de las especies. Por otra parte, algunas de las especies comúnes de escafópodos en el área no están aquí representados. Algunas de las especies tienen registros fósiles extensos, y en *Entalina tetragona* y *Antalis inaequicostata* se discuten problemas relacionados con su sinonimia y biogeografía histórica.

KEY WORDS: Scaphopoda, systematic biogeography, Iberian Peninsula and Balearic Islands
PALABRAS CLAVE: Escafópodos, sistemática biogeografía, península Ibérica e islas Baleares.

INTRODUCTION

The main purpose of this paper is the systematic treatment of Scaphopoda collected by recent sampling cruises of the Fauna Ibérica programme along the Spanish coasts. The cruises Fauna I (July, 1989), Fauna II (June - July, 1991) and Fauna III (June - July, 1994) covered the Sea of Alborán, the Gulf of Cádiz, the Bay of Biscay, the Atlantic coast off South Galicia, and the waters around the Balearic Islands. Scaphopod specimens are represented in 29 stations of these cruises. A list of stations of the "Fauna I" cruise is already published (TEMPLADO, GUERRA, BEDOYA, MORENO, REMÓN, MALDONADO AND RAMOS,

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1993); publications with the stations of the remaining cruises are in preparation (Templado, pers. comm.). Sources of primary faunistic information on Scaphopoda are reports of the marine expeditions "Travailleur" and "Talisman" (LOCARD, 1898), "Porcupine", "Valorous" and two smaller cruises (JEFFREYS 1870, 1877, 1882), and ALZURIA (1986, 1987). Faunistic and systematic accounts of the Eastern Pyrenean Seas were made by BUCQUOY, DAUTZENBERG AND DOLLFUS (1882) and MARS (1965). The only synopsis of Iberian and Balearic molluscs to date (HIDALGO, 1917) also includes Scaphopoda. The fundamental monography of PILSBRY AND SHARP (1897), the comprehensive studies of CAPROTTI (1965, 1968, 1979), and the classification of higher taxa of STEINER (1992, 1996) and SCARABINO (1995) form the basis of the systematic treatment. Complementary information on synonyms is drawn from MONTEROSATO (1875) and STORK (1934). The material studied in this paper is deposited in the Museo Nacional de Ciencias Naturales, Madrid.

SYSTEMATIC ACCOUNT

The samples revealed 12 species from 7 genera and 5 families. Both orders of Scaphopoda, Dentaliida and Gadilida are represented, with 8 and 4 species respectively. Each species is listed with synonyms, original description, type locality, distribution in the present material (with distribution maps) and as reported in the literature, and with the earliest fossil occurrence. The numbers of empty shells (e) and of shells with soft body (b) are given for each station.

Order DENTALIIDA Da Costa, 1776
Family DENTALIIDAE Gray, 1847
Genus *Antalis* H. and A. Adams, 1854

Antalis agilis (M. Sars, 1872) (Figs. 1, 4A)

Synonyms
Dentalium incertum Philippi 1844, *Enum. Moll. Sicil.* II: 207, non Deshayes 1825.
Dentalium abyssorum var. *agilis* Jeffreys 1870, *Ann. Mag. N. Hist.* Ser. 4 VI: 74.
Dentalium agile M. Sars 1872, *Some remarkable forms etc., Christiania* 1872: 34.
Dentalium fusticulus Brugnone 1876, *Misc. Malac.* II: 21.
Dentalium vagina Jeffreys 1877, *Ann. Mag. N. Hist.* Ser. 4, XIX: 155.
Antalis agilis (M. Sars): G. O. Sars 1878, *Moll. Reg. Arct. Norv., Christiania* 1878: 102.
Dentalium (Antalis) calabrum Crema 1910, p. 68.

Original description: Shell slender, very narrow, slightly curved, almost straight, gradually attenuated towards the apex. White, faint luster, posterior part frequently darker. Apex very narrow, obliquely truncated, with a tolerably deep incision and a short, hardly protruding supplementary tube. Shell surface with circular growth lines, rarely longitudinally striated in the posterior part, the striae being little distinct and never prominent ribs. [...] Largest shell 58 mm long and 4 mm in diameter, 1 mm at the apex.

Type locality: Lofoten Islands, North Atlantic, at 360-540m.

Present material: 5 stations; Gulf of Cádiz, 500-546 m (76A: 1b, 20e; 77A: 3b); Cape Finisterre, 129-133 m (91A: 1b); Biscay, 540-1025 m (124A: 2b, 9e; 159A: 2b, 14e).

Reported distribution: North Atlantic: Portugal to Lofoten, Halifax to Cuba, Gulf of Mexico, Azores; Mediterranean; ?Red Sea; 60-5000 m.

Earliest fossil: Pliocene.

Remarks: The largest specimen from station 159A is 65 mm long, which exceeds indications of SARS (1872), PILSBRY AND SHARP (1897) and CAPROTTI (1965), but matches those of LOCARD (1898). There are no shells with apical slits in the present material, but most of the specimens are empty shells and fragments. The shell surface in the apical region may be eroded by boring organisms even in live animals. The shell then has a chalky and often crackled aspect, as was also remarked by SARS (1872). Young individuals are often more or less distinctly ribbed near the apex. The ribs intercalate to about 20 in number and then gradually become obsolete. The younger parts of the shell (towards the anterior opening) with an intact surface are glossy and bear closely spaced growth lines. LOCARD (1898) distinguished a number of varieties according to size, curvature and sculpture. *Antalis panorma* (Chenu, 1842-47), similar in size and shape to *A. agilis* and reported from the Mediterranean and the Bay of Biscay, differs in being more curved and having a more solid shell with 12 narrow but pronounced primary ribs.

Some of the shells from station 76A have bore holes of naticid gastropods being, apart from different fishes, important predators of scaphopods in the Mediterranean.

Antalis entalis (Linné, 1758) (Figs. 1, 4B)

Synonyms
Dentalium entalis Linné 1758, *Syst. Nat.* (10): 785.
Dentalium entalum L.: Blainville 1819, *Dict. Sc. Nat.* XIII: 70.
Dentalium labiatum Brown 1827, *Ill. Conch. Gr. Brit. and Irel.*: pl. 1, fig. 4.
Dentalium striolatum Stimpson 1851, *Proc. Bost. Soc. Nat. Hist.* IV: 114. non Jeffreys, Watson, Sars, Risso.
Entalis striolata (Stimpson 1851): Gould-Binney 1870, Invert. of Mass.: 266.

Original description: Shell smooth, moderately curved, continuous, not fractured.

Type locality: Atlantic Ocean.

Present material: 2 stations; La Coruña, 151-152 m (101A: 1e); Biscay, 119-122 m (112DH: 2e).

Reported distribution: North Atlantic from Spain north to Spitzbergen and Maine, Massachusetts to Bay of Fundy; 6-3500 m.

Earliest fossil: Pliocene.

Remarks: The shell is up to 42 mm long, solid, white, sometimes glossy, moderately curved but in the apical region, the wider, anterior part of the shell being only slightly curved. The shell surface is smooth, very fine longitudinal striae may be present in the apical region only. Towards the anterior opening growth lines become more distinct. There may be a shallow apical notch on the convex side.

This species is infrequently cited from the Mediterranean as well, due to confusion with the apically striated *Antalis vulgaris*. However, HIDALGO (1917) retains Gibraltar and Mataró/Catalunya as localities for *A. entalis*.

Antalis dentalis (Linné 1766) (Figs. 1, 4C)

Synonyms
Dentalium dentalis Linné 1766, *Syst. Nat.* XII: 1263.
Dentalium dentale L.: Locard 1886, *Ann. Soc. Agricult., Lyon* Ser. 5, IX: 145.
Dentalium linnaeum Locard 1886, *Ann, Soc. Agricult., Lyon* Ser. 5, IX: 145.
Dentalium mutabile Döderlin in Hörnes 1856, *Abhandl. K. -K. Geol. Reichsanst.* III: 654.

Original description: Shell striated, moderately curved, fractured.

Type locality: Mediterranean Sea.

Present material: 1 station; Gulf of Cádiz, 13-15 m (71A: 1e).

Reported distribution: Mediterranean Sea, East Atlantic from Galicia to Cape of Good Hope (?), Azores, Canary Islands; 0-300 m.

Earliest fossil: Miocene.

Remarks: This rather small species is up to 24 mm long (13 mm from station 71A), mostly white, only the apex sometimes with a rose tinge. There are about 10 sharp and narrow primary ribs, becoming doubled by intercalation towards the anterior opening. The secondary ribs are of about the same height as the primary ribs. The intercostal spaces are much wider than the ribs, and smooth except for widely spaced growth lines. *Antalis dentalis* is often confused with *A. inaequicostata* (see below).

Antalis inaequicostata (Dautzenberg, 1891) (Figs. 1, 4D)

Synonyms

Dentalium dentalis Lamarck 1818, *Anim. sans vert.* V: 344; Deshayes 1825, *Anat. et Monogr. du genre Dentale*: 33; Risso 1826, *Hist. Nat. Europ. Merid.* IV: 398; Philippi 1836, *Enum. Moll. Sicil.* I: 243; Jeffreys 1870, *Ann. Mag. Nat. Hist.* VI: 10; Monterosato 1872, *Not. Int. alle conch. Medit.*: 28; non Linné 1766.

Dentalium fasciatum Lamarck 1818, *Anim. sans vert.* V: 343; non Gmelin 1790

Dentalium pseudo-antalis Scacchi 1836, *Catal. Conch. Regni Neap.*: 17; non Lamarck 1818

Dentalium novem-costatum Réquien 1848, *Coq. de Corse*: 90; non Lamarck 1818.

Dentalium novemcostatum var. *tenuis* Monterosato 1878, *Enum. et Sinon.*: 16; non Lamarck 1818.

Dentalium novemcostatum Réquien: Monterosato 1884, *Nom. Gen. e Spec.*: 31; non Lamarck 1818.

Dentalium alternans Bucquoy, Dautzenberg and Dollfus 1891, *Moll. Mar. Roussillon* I: 561; non Chenu 1842.

Dentalium inaequicostatum Dautzenberg 1891, *Mem. Zool. Soc. France* 1891: 53.

Antale novemcostatum (Réquien): Sacco 1897, *Moll. terr. terz. Piemonte e delle Liguria* XXII: 104.

Dentalium (Antalis) inaequicostatum B. D. D.: Pilsbry and Sharp 1897-98, Man. Conch. XVII: 52. Caprotti 1965, *Atti. Soc. Ital. Sci. Nat. Milano* 105: 343.

Dentalium novemcostatum var. *inaequicostata* Fantinet 1959, *Serv. Carte Geol. Algérie* 1: 46.

Dentalium (Antalis) novemcostatum Réquien: Caprotti 1961, *Atti. Soc. Ital. Sci. Nat. Milano* 100: 353.

Dentalium (Antalis) mutabile inaequicostatum Dautzenberg: Caprotti 1979, *Boll. Malacol. Milano* 15: 233.

Original description: Shell solid, opaque, slightly to moderately curved, straightening towards the anterior aperture. Sculpture of 9 or 10 primary ribs alternating with same number of wider and less protruding secondary ribs. All ribs become obsolete towards the anterior. Numerous transverse growth lines, sometimes with irregular fractures or interruptions. Anterior shell aperture slightly polygonal. Posterior aperture truncated, polygonal, with an oval, short central pipe. No slit or notch. Colour light rose, more intense at the posterior end, transversal bands of lighter and darker colour. Shell 35 mm long, 5 mm at anterior aperture.

Type locality: Mediterranean Sea.

Present material: 4 stations; Gulf of Cádiz, 13-28 m (44A: 2e; 66A: 9b, 3e; 69A: 1e; 71A: about 10b, many empty shells).

Reported distribution: Mediterranean from Greece to Algeria; 5-120m.

Earliest fossil: Miocene (BUCQUOY *ET AL.*, 1886) or Pliocene (CAPROTTI, 1979).

Remarks: This species is extremely variable in its longitudinal sculpture causing considerable confusion in studies of both fossil and recent scapho-

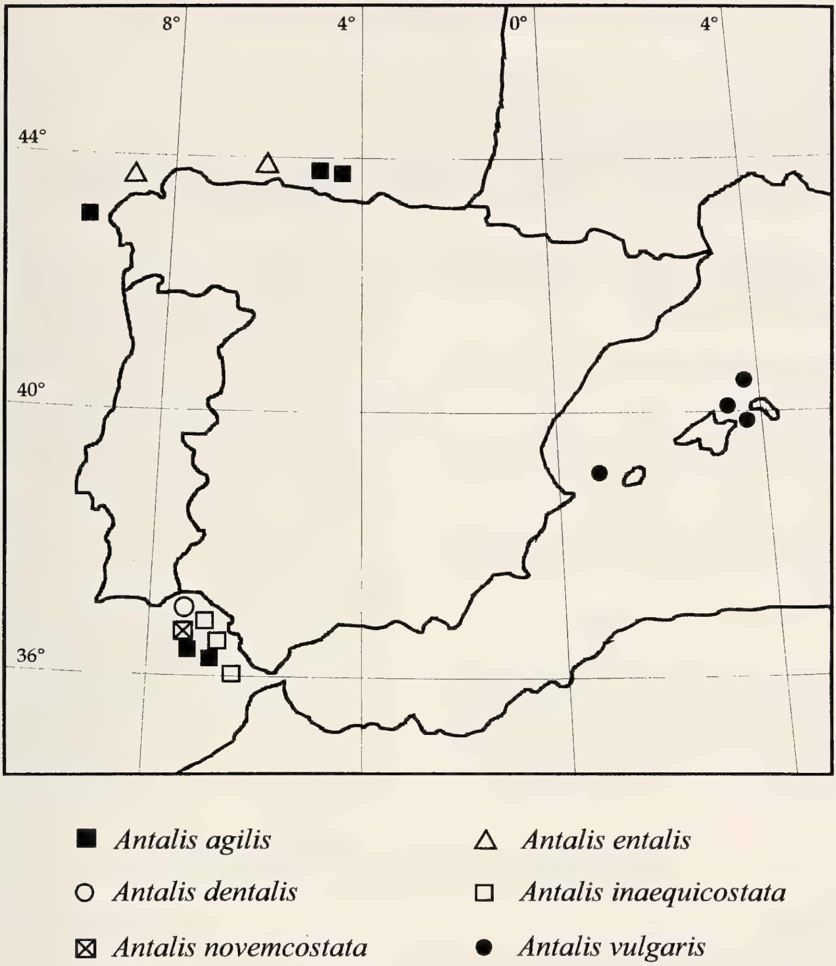


Figure 1. Localities where *Antalis agilis, A. entalis, A. dentalis, A. inaequicostata, A. novemcostata,* and *A. vulgaris* were collected.
Figura 1. Localidades donde se encontraron las especies Antalis agilis, A. entalis, A. dentalis, A. inaequicostata, A. novemcostata *y* A. vulgaris.

pods. Small individuals of this species closely resemble *Antalis dentalis.* The latter differs, however, in having conspicuous transversal striae between the ribs, the ribs themselves are less acute, and the intercostal space is not as wide. If PILSBRY AND SHARP (1897-98, p. 52) describe "... 9-12 strong primary ribs towards the apex, narrower than their intervals... " for *A. inaequicostata,* they obviously did not consider direct comparison with *A. dentalis.* The atlantic *A. novemcostata* is stouter and has more conspicuous transverse striae.

Many of the empty shells shows characteristic signs of sipunculid occupation. *Phascolion strombus* (Montagu, 1804) is known to close the anterior openings of scaphopod and other mollusc shells by agglutinations of sediment, leaving open only a small tube for their introvert (TÉTRY, 1959).

Antalis novemcostata (Lamarck, 1818) (Figs. 1, 4E)

Synonyms
Dentalium novemcostatum Lamarck 1818, *Anim. sans vert.*, V: 344.
Dentalium dentalis Risso 1826, *Hist. Nat. Europ. Mérid.*, IV: 398.
Dentalium dentale Risso: Weinkauff 1862 (partim), *J. Conch.*, X: 364.
Antale novemcostatum (Lamarck): Sacco 1896, *Boll. Mus. Zool. Anat. Comp. Univ. Torino*, XI: 97.
Dentalium (Antalis) novemcostatum (Lamarck): Pilsbry and Sharp 1897-98, *Man. Conch.*, 17: 51

Original description: Shell small, greenish-white, with nine ribs, subdecussate transverse striae.

Type locality: Atlantic coast near La Rochelle.

Present material: 1 station, Gulf of Cádiz, 110-112 m (69A: 1e).

Reported distribution: East Atlantic from La Rochelle to South Spain; 20-300 m.

Earliest fossil: Pliocene.

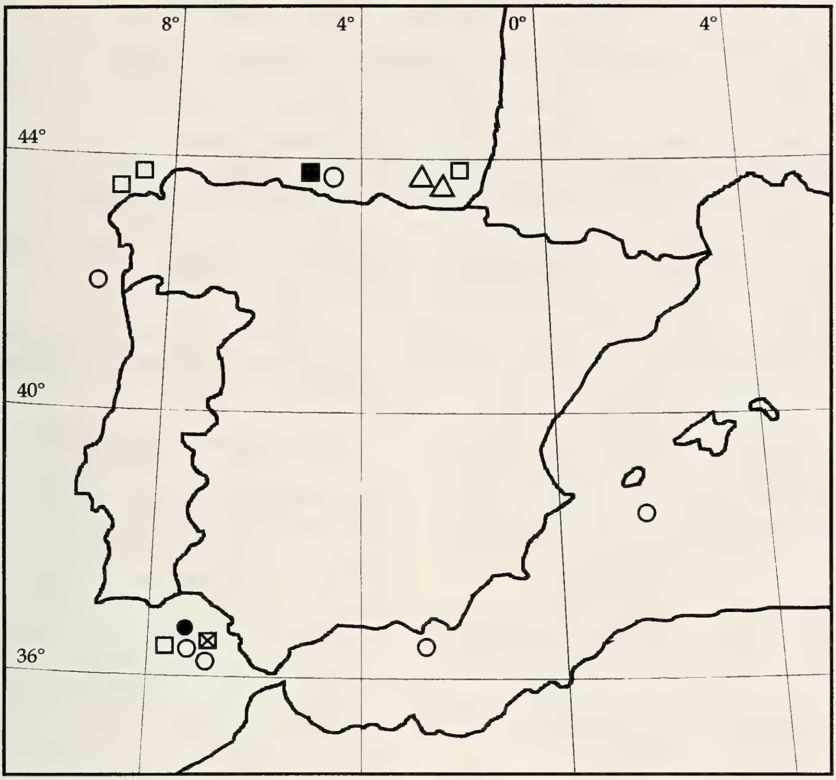
Remarks: The rather stout shell is up to 32 mm long and has 8 to 10 rounded ribs decreasing in heigth towards the anterior opening. The intercostal spaces are more concave than in the other *Antalis* species of the region and show faint longitudinal striae. Transverse striae are not always developed, although BUCQUOY *ET AL.* (1886) and CAPROTTI (1965) take the strong transverse sculpture as an important character to distinguish *A. novemcostata* from the mediterranean *A. inaequicostata*. The apex often has a plug with a central pipe in larger specimens.

Antalis novemcostata seems to be living on the european Atlantic coast only, although HIDALGO (1917) lists several mediterranean locations for this species. This seems to be due to misidentifications of *A. inaequicostata* (CAPROTTI, 1961, 1965; MARS, 1965). According to CAPROTTI (1965), the extremely rare *A. novem-costatum* from the Italian Pliocene could be intermediate between *A. inaequicostata* and *A. novemcostata*.

Antalis vulgaris (Da Costa, 1778) (Figs. 1, 4F)

Synonyms
Dentale vulgare Da Costa 1778, *Brit. Conch.*: 24.
Dentalium fasciatum Gmelin 1791, *Syst. Nat.*, 13: 3737.
Dentalium striatum Montagu 1803, *Test. Brit.*, II: 492, non Born 1780, *Test. Mus. Caes. Vindob.*: 431.
Dentalium tarentinum Lamarck 1818, *Anim. sans vert.*, V: 345. Forbes and Henley 1853, *Hist. Brit. Moll.*, II: 451. Sowerby 1860, *Thes. Conch.*, II: 100. Jeffreys 1882, *Brit. Conch.*, II: 195. Clessin 1896, *Conchyl. Cab.*: 3.
Dentalium politum Blainville 1819, *Dict. Sci. Nat.*, XIII: 70. Turton 1819 (partim), *Conch. Dict. Brit. Sh.*: 38.
Dentalium labiatum Turton 1819 (partim), *Conch. Dict. Brit. Sh.*: 38. Brown 1827, *Illustr. Conch. Gr. Brit.*: 117.
Dentalium striolatum Risso 1826, *Hist. Nat. Europ. Mérid.*, IV: 398.
Dentalium multistriatum Risso 1826, *Hist. Nat. Europ. Mérid.*, IV: 398, non Deshayes 1825, *Anat. et Monogr. du genre Dentale.*
Dentalium affine Biondi 1859, *Atti Accad. Gioenia Sci. Nat.* (2), XIV: 120.

Original description: *Dentalium* with a slender, smooth, glossy, subarcuated shell, tapering to a small point, pervious: sometimes marked with a few circular wrinkles or annulations: colour white or yellowish. Length an inch and a half [38 mm]; diameter at the larger end two-tenths of an inch [5 mm]; and one fourth as much [1.25 mm] at the smaller end. [...] A variety is marked with dusky bands; and sometimes a little striated towards the point.



■ *Fissidentalium capillosum* △ *Episiphon filum*
○ *Entalina tetragona* □ *Pulsellum lofotense*
⊠ *Dischides politus* ● *Cadulus jeffreysi*

Figure 2. Localities where *Fissidentalium capillosum, Episiphon filum, Entalina tetragona, Pulsellum lofotense, Dischides politus,* and *Cadulus jeffreysi* were collected.
Figura 2. Localidades donde se encontraron las especies Fissidentalium capillosum, Episiphon filum, Entalina tetragona, Pulsellum lofotense, Dischides politus *y* Cadulus jeffreysi.

Type locality: British shores, especially Scilly Islands, Cornwall, Devonshire, Hampshire.

Present material: 5 stations; Biscay, 119-122 m (112DH: 1e); Balearic Islands, 5-59 m (190B: 2e; 192A: 1b; 203B: 1e; 258B: 3b).

Reported distribution: Mediterranean Sea and East Atlantic Ocean; 5-1100 m.

Earliest fossil: Miocene.

Remarks: The shell is up to 60 mm long, white with a rose-coloured apex, rather broad, and moderately curved in the posterior half. There are about 30 longitudinal striae near the apex, obliterating gradually towards the anterior opening. The apical opening is entire and may have a plug with a short central pipe.

Genus *Fissidentalium* Fischer, 1885

Fissidentalium capillosum (Jeffreys, 1876) (Figs. 2, 4G)

Synonyms
Dentalium capillosum Jeffreys 1876, *Proc. Roy. Soc.*, 25: 185. (nomen nudum)
Dentalium capillosum Jeffreys: Jeffreys 1877, *Ann. Mag. Nat. Hist. Ser.* 4, 19: 153.
Dentalium (Fissidentalium) capillosum Jeffreys: Pilsbry and Sharp 1897-98, *Man. Conch.*, 17: 77.

Original description: Shell tapering to a fine point, slightly curved, rather solid, opaque, and mostly lusterless; sculpture: numerous and sharp (not rounded) longitudinal striae, some of which are intermediate and smaller than the rest; they disappear towards the posterior or narrow end, which is quite smooth and glossy for a quarter of an inch [6.4 mm]; colour whitish; margin at the posterior end having a short and narrow notch. L [length]: 1.4 [35.6 mm]. B [maximum diameter]: 0.15 [3.8 mm]. (...) This appears to attain a size considerably exceeding that given in the above description, as fragments measure nearly 0. 4 inch [10 mm] in breadth.

Type locality: North Atlantic, Valorous st. 12, 13, 16; 1242-3213 m.

Present material: 1 station; Biscay, 925-1025 m (159A: 5e).

Reported distribution: North Atlantic, Caribbean Sea to Portugal, Azores to Hebrides; 400-3500 m.

Earliest fossil: No fossil record.

Remarks: This species can be 81 mm long. The shell is white or grey and may be somewhat eroded. There are about 65 fine ribs throughout most of the length. Pilsbry and SHARP (1897-98) supplement JEFFREYS' (1877) description saying that the ribs are sharply cut but rounded on the top. This is particularly obvious in the anterior part of the shell where the ribs become wider.

Family GADILINIDAE Chistikov, 1975
Subfamiliy EPISIPHONINAE Chistikov, 1975
Genus *Episiphon* Pilsbry and Sharp, 1897-98

Episiphon filum (Sowerby, 1860) (Figs. 2, 4H)

Synonyms
Dentalium filum Sowerby 1860, *Thes. Conch.*, III: 89.
Dentalium gracile Jeffreys 1870, *Ann. Mag. Nat. Hist.* (4), VI: 74. Fischer 1873, *Journ. Conchyl.*: 140.
Pseudantalis filum (Sowerby): Monterosato 1884, *Nom. Gen. Spec. Conch. Medit.*: 33.
Dentalium rufescens Weinkauff 1868 (partim), *Conch. Mittelm.*, II: 420.

Original description: Shell slender, very narrow, thin, finely pointed, mantle reddish brown, apex entire.

Type locality: Gibraltar.

Present material: 2 stations; Biscay, 104-132 m (152A: 2b, 1e; 153A: 2b).

Reported distribution: North Atlantic from Florida to Cape Hatteras, Algeria to Biscay; Mediterranean Sea from Aegean to Gibraltar; 20-4784 m.

Earliest fossil: Miocene.

Remarks: This is a very characteristic species, being very narrow, hardly tapering and almost straight. The length is up to 13 mm. The shell is white and glossy, semitransparent and extremely fragile. The sculpture consists of growth lines only. Typical for the genus is a long pipe at the apex continuous with the shell. It may be wanting because of its fragility.

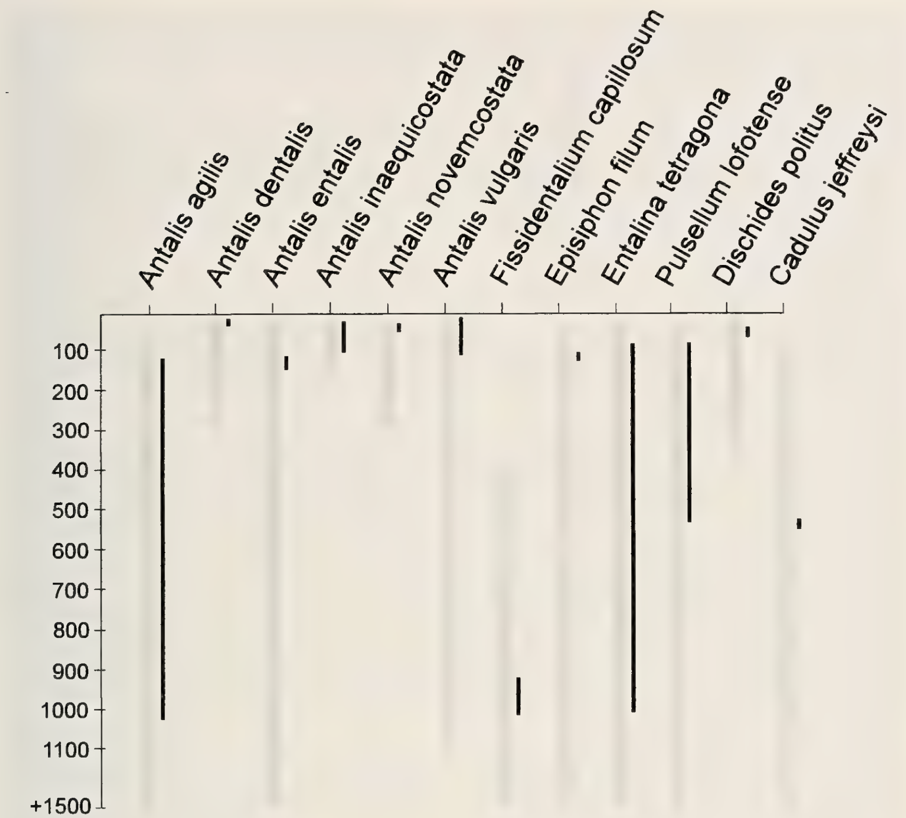


Figure 3. Bathymetric ranges of species reported in literature (shaded) and in the present material (black).
Figura 3. Rangos batimétricos de las especies: datos bibliográficos (gris), datos del presente material (negro).

Order GADILIDA Starobogatov, 1982
Suborder ENTALIMORPHA Steiner, 1992
Family ENTALINIDAE Chistikov, 1979
Subfamily ENTALININAE Chistikov, 1979
Genus *Entalina* Monterosato, 1872

Entalina tetragona (Brocchi, 1814) (Figs. 2, 5A)

Synonyms

Dentalium tetragonum Brocchi 1814, *Conch. foss. subapen., Milano*: 627.
Dentalium quinquangulare Forbes 1844, Re*p. Brit. Ass. Adv. Sci.* for 1844: 188.
Siphonodentalium pentagonum M. Sars 1865, *Forh. Videsk. Selsk. Christiania* 1864: 307.
Dentalium quinquangulatum Reeve 1872, *Conch. Icon.*: pl. 5, fig 45.
Siphonodentalium quinquangulare (Forbes): Jeffreys 1867, *Ann. Mag. Nat. Hist.* Ser. 3, XX: 251. Weinkauff 1868, *Conch. Mittelm.*, II: 421. Locard 1886, *Ann, Soc. Agricult., Lyon* Ser. 5, IX: 149. Dautzenberg 1891, *Mem. Soc. Zool. France,* IV: 609. Friele and Grieg 1901, *Norv. N. Atlant. Exp. etc., Christiania* 1901, Mollusca III: 50.
Siphonentalis tetragona (Brocchi): G. O. Sars 1878, *Moll. Reg. Arct. Norv., Christiania* 1878: 105.

Siphodentalium tetragonum (Brocchi): Norman 1879, *J. Conch., London*, 2: 49.
Entalina tetragona (Brocchi): Monterosato 1880, *Bull. Soc. Malac. Ital.*, VI: 64. Caprotti 1961, *Atti Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano*, Vol. C, IV: 356.
Siphodentalium quinquangulare (Forbes): Jeffreys 1882, *Proc. Zool. Soc. London*, 1882: 662.
Siphonentalis quinquangularis (Forbes): Carus 1889, *Prodr. faunae Medit.*, II: 176.
Pulsellum quinquangulare (Forbes): Norman 1893, *Ann. Mag. Nat. Hist.* Ser. 6, XII: 344, 362.
Entalina quinquangularis (Forbes): Hidalgo 1917, *Trab. Mus. Nac. Cienc. Nat.* Ser Zool. 30: 306. Chistikov and Sagaidachniy 1982, *Zool. Zhurn.*, 60: 38.

Original description: Shell four-angled, finely longitudinally striated, sides weakly carinated.

Type locality: Pliocene of Italy (BROCCHI, 1814), Aegean Sea (FORBES, 1844).

Present material: 6 stations; Mediterranean, 1001-1005 m (247A: 1e); Sea of Alborán, 276-306 m (15A: 2e); Gulf of Cádiz, 500-546 m (76A: 3e; 77A: 2e); Galicia, 81-84 m (86DL: 1b), Biscay, 540-543 m (124A: 5b, 15e).

Reported distribution: Mediterranean, East Atlantic from Biscay to Northern Norway; 10-2664 m.

Earliest fossil: Miocene.

Remarks: The shell is strongly curved, at least in the apical half. It has five primary ribs, four of them forming almost right angles, the fifth rib on the midline of the concave side forms an obtuse angle. In specimens larger than about 10 mm, 3 - 25 secondary ribs gradually appear, the pentagonal form of the cross-section smoothing out to become subcircular. The anterior opening is oblique, the apex simple and entire. The shells may be up to 93 mm long but are usually around 15 mm.

There is some confusion in the European species and the use of the names *tetragona* Brocchi, *pentagona* Sars and *quinquangularis* Forbes. BROCCHI (1814) described *tetragona* as a Pliocene fossil from Piemont and the Vienna Basin. FORBES (1844) described the extant species from the Aegean Sea as *quinquangularis*. MICHAEL SARS (1865) described *pentagona* from the Norwegian coasts, without referring to either Brocchi or Forbes. His son, G. O. SARS (1878) considers *pentagona* and *quinquangularis* as junior synonyms of *tetragona*. MONTEROSATO (1880) comes to the same conclusion claiming the fossil and recent mediterranean species being identical. JEFFREYS (1870, 1882), however, is of different opinion and gives priority to *quinquangularis* for the recent Atlantic and Mediterranean form. PILSBRY AND SHARP (1897-98), LOCARD (1898) and FRIELE AND GRIEG (1901) agree with this view.

CAPROTTI (1968), finally, comparing recent specimens with the type material, confirmes the synonymity of *quinquangularis* and *tetragona*, stressing the priority of Brocchi´s name. Later, CHISTIKOV AND SAGAIDACHNIY (1982), however, not only separate *tetragona* and *quinquangularis*, but also split the latter into the Mediterranean *quinquangularis* and the Atlantic *pentagona* on grounds of shell and radula characters. However, they do not include fossil specimens in their study.

Suborder GADILIMORPHA Steiner, 1992
Family PULSELLIDAE Scarabino in Boss, 1982
Genus *Pulsellum* Stoliczka, 1868
Pulsellum lofotense (M. Sars, 1865) (Figs. 2, 5B)

Synonyms
Siphonodentalium lofotense M. Sars 1865, *Forh. Videsk. Selsk. Christiania* 1864: 297.
Siphonentalis lofotensis (M. Sars): G. O. Sars 1878, *Moll. Reg. Arct. Norv., Christiania* 1878: 104. Monterosato 1884, *Nom. Gen. Spec. Conch. Medit.*: 33.

Figure 4. A: *Antalis agilis*; B: *Antalis entalis*; C: *Antalis dentalis*; D: *Antalis inaequicostata*; E: *Antalis novemcostata*; F: *Antalis vulgaris*; G: *Fissidentalium capillosum*; H: *Episiphon filum*. Scale bars, A, G: 10 mm; B-F: 2 mm; H: 1 mm.

Figura 4. A: Antalis agilis*; B:* Antalis entalis*; C:* Antalis dentalis*; D:* Antalis inaequicostata*; E:* Antalis novemcostata*; F:* Antalis vulgaris*; G:* Fissidentalium capillosum*; H:* Episiphon filum. *Escalas, A, G: 10 mm; B-F: 2 mm; H: 1 mm.*

Siphodentalium lofotense M. Sars: Jeffreys 1882, *Ann. Mag. Nat. Hist.*, Ser. 5, XI: 395.
Siphonodentalium (Pulsellum) lofotense M. Sars: Pilsbry and Sharp 1897-98, *Man. Conch.*, 17: 138.
Siphonodentalium lofotensis M. Sars: Stork 1934, *Thalassia*, 1: 10.
Pulsellum lofotensis (M. Sars): Emerson 1962, *Journ. Paleontol.* 36: 475.

Original description: Shell smooth, moderately curved, anteriorly wide and tapering to the posterior, white, walls transparent or semitransparent, thin, shiny, very fine and dense obliquely transverse growth lines well visible, posterior shell margin entire [plain]. Length 5-6 mm, basal width 0.66 mm, apical about 0.33 mm. [Description of soft body omitted.]

Type locality: Lofoten Isl., Norway; 90-216 m.

Present material: 4 stations; Gulf of Cádiz, 535-546 m (76A: 3e); Galicia, 80-120 m (168A: 3e; 171A: 3e); Biscay, 129-132 m (153A: 5b, about 20e).

Reported distribution: Mediterranean Sea; North Atlantic from Spain to Finmark, Ireland, New England; 26-3500 m.

Earliest fossil: Pliocene.

Remarks: The small shell is rather fragile in the anterior third and easily breaks into cylindric fragments upon handling. Breakage occurs along the oblique growth lines. The anterior opening is circular as the apical opening but slightly oblique. Most live animals have perfectly transparent shells, empty shells are opaque. The apical rim is always entire without notches or lobes, although JEFFREYS (1882) mentions specimens with regularly jagged tips. This may have been a siphonodentaliid species, also because he did not see a bulbous larval shell, which is well developed in *Pulsellum lofotense* (Steiner, 1995).

Family GADILIDAE Stoliczka, 1868
Subfamily SIPHONODENTALIINAE Simroth, 1894
Genus *Dischides* Jeffreys, 1867

Dischides politus (Wood, 1842) (Figs. 2, 5C)

Synonyms
Ditrupa polita Wood 1842, *Ann. Mag. Nat. Hist.*, 9: 459.
Dentalium coarctatum Philippi 1844, *Enum. Moll. Sicil.*, II: 208, non Lamarck 1818, *Anim. sans Vert.*, 5: 346.
Dentalium laevigatum de Rayneval, Hecke and Ponzi 1854, *Cat. Foss. Mont Mario, Versailles,* non Schlotheim 1830.
Dentalium bifissum Jeffreys 1867, *Ann. Mag. Nat. Hist.*, Ser. 3, XX: 251. Weinkauff 1868, *Conch. Mittelm.*, II: 421. Monterosato 1884, *Nom. Gen. Spec. Conch. Medit.*: 34.
Dischides olivi Jeffreys 1870, *Ann. Mag. Nat. Hist.*, Ser. 4, VI: 73.
Dischides bifissus (Jeffreys): Jeffreys 1882, *Proc. Zool. Soc. London*, 1882: 663.
Cadulus politus (Wood): Pilsbry and Sharp 1897-98, *Man. Conch.*, 17: 144. Stork 1934, *Thalassia*, 1: 9.

Original description: Shell slightly arcuated, thin, smooth, subcylindrical; anterior opening plain, posterior cleft, bilateral, with unequal terminations. The body of the [...] shell is not inflated or enlarged like that of *Dentalium gadus*, but has the posterior opening laterally cleft, somewhat resembling that of *Dentalium coarctatum* Deshayes [...] but the dorsal part of the posterior end of this fossil is produced beyond the edge beneath and rounded, the ventral edge is shorter and truncated, an enamel-like polish covers the exterior, and was probably when inhabited subhyaline, but is now opaque. Length half an inch [12.7 mm] nearly.

Type locality: Coralline Crag, England (Pliocene).

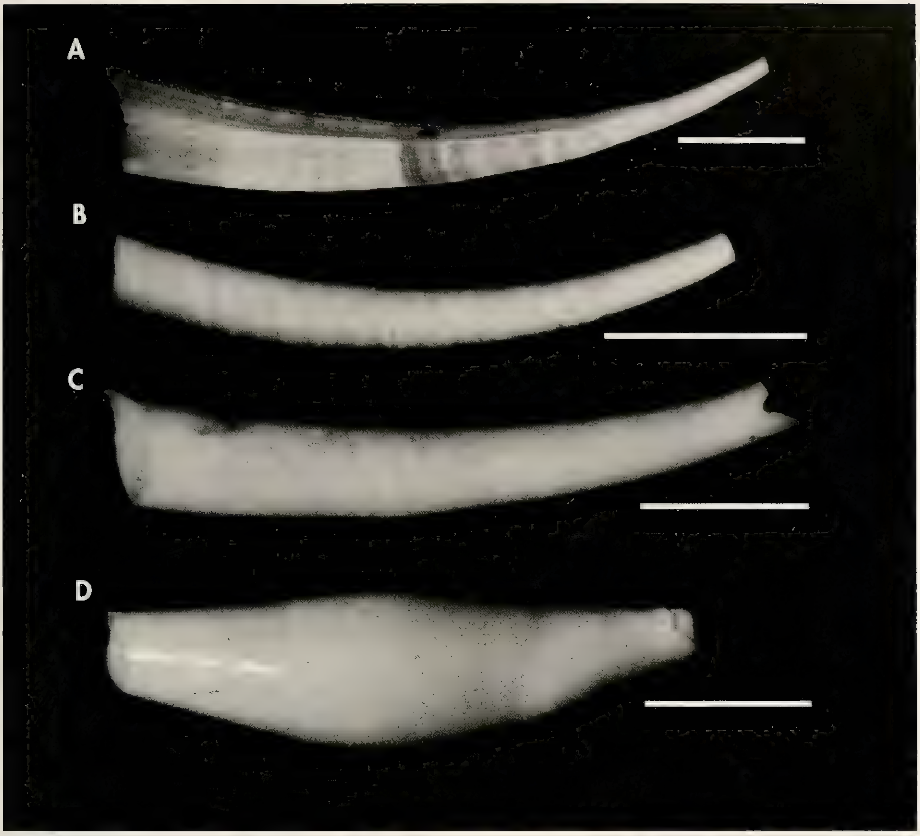


Figure 5. A: *Entalina tetragona*; B: *Pulsellum lofotense*; C: *Dischides politus*; D: *Cadulus jeffreysi*. Scale bars 1 mm.
Figura 5. A: Entalina tetragona*; B:* Pulsellum lofotense*; C:* Dischides politus*; D:* Cadulus jeffreysi. *Escalas 1 mm.*

Present material: 1 station; Gulf of Cádiz, Trafalgar, 34 m (58A: 1e).

Reported distribution: Northeast Atlantic from Marocco to Biscay, Mediterranean; 9-324 m.

Earliest fossil: Pliocene.

Remarks: The recent members of this species attain maximum lengths of 7 mm. The shell is white, glossy, moderately curved and only slightly tapering. The sculpture consists of growth lines only. The greatest diameter of the shell lies just behind the anterior opening. The posterior opening has two lateral notches producing a dorsal and a ventral lobe. Tubes of the serpulid polychaete *Ditrupa* sp. must not be confused with *Dischides politus*. The polychaete tubes are often reddish brown in colour, the outer layer has a semitransparent aspect. They are sharply constricted at the anterior opening and lack growth lines.

Dischides has repeatedly been changing between subgenus and genus status. It was recently confirmed in its generic rank and transferred to the subfamily Siphonodentaliinae by SCARABINO (1995).

Subfamily GADILINAE Stoliczka, 1868
Genus *Cadulus* Philippi, 1844
Cadulus jeffreysi (Monterosato, 1875) (Figs. 2, 5D)

Synonyms
Helonyx jeffreysi Monterosato 1875
Cadulus jeffreysi (Monterosato): Jeffreys 1882, Verrill 1882, Pilsbry and Sharp 1897-98, Muus 1959
Cadulus propinquus Verrill 1885, non G. O. Sars
Cadulus subfusiformis Stork 1934, non M. Sars

Original description: Anterior aperture obliquely truncated, base or [?and] posterior aperture compressed, slightly deformed at each side.

Type locality: Aegean Sea, 234-450 m.

Present material: 1 station; Gulf of Cádiz, 535-546 m (76A: 18e).

Depth range: 535-546 m.

Reported distribution: Mediterranean; North Atlantic from Canary Is., Biscay to Ireland and Norway, West Atlantic from Martha´s Vineyard to Barbados, South Atlantic at St. Helena; 90-2200 m.

Earliest fossil: Pliocene

Remarks: Shell small, smooth and shiny, moderately curved, with a conspicuous swelling just anterior to the middle; ventral side regularly curved, dorsal side with distinct convex area due to the swelling; anterior shell aperture obliquely truncated facing downwards, slightly laterally compressed; posterior aperture without lobes, dorsoventrally depressed.

This species may be confused with *Cadulus subfusiformis* (M. Sars 1865). It differs in being larger, conspicuously swollen near the middle of the shell and having a distinct convex area in the dorsal line. The anterior aperture is slightly laterally compressed, the posterior aperture dorsoventrally depressed, while *C. subfusiformis* has a faintly dorsoventrally depressed anterior end and a round posterior one.

DISCUSSION

Of the 19 valid species listed for the Iberian coasts by HIDALGO (1917), 12 are represented in the present material. Taking into account the recent finding of the Eastern Mediterranean species *Antalis rossati* near Barcelona (Alzuria, 1986) and the deep-water Biscayan material of the "Talisman", "Travailleur" (LOCARD, 1898) and "Valorous" (JEFFREYS, 1877) expeditions, the species list of Iberian scaphopods grows to 31. Species treated in these reports but not present in this material are listed in Table I.

The present findings provide no biogeographic novelties. Species living in both the Atlantic and Mediterranen Sea are *Antalis agilis, A. dentalis, A. vulgaris, Episiphon filum, Entalina tetragona, Pulsellum lofotense, Dischides politus* and *Cadulus jeffreysi*. The only typical Mediterranean forms in the material is *A. inaequicostata*. This latter shallow-water form extends, however, beyond the Strait of Gibraltar into the Gulf of Cádiz. On the other hand, *A. entalis, A. novemcostata* and *Fissidentalium capillosum* are known from Atlantic waters only.

Comparing the bathymetric data of this material with reported ranges (Fig. 3), only *Antalis agilis, A. inaequicostata* and *Entalina tetragona* cover the greater part of their ranges. Most of the other species are found a one or two stations only, which may explain their relatively restricted bathymetric occurrence.

CAPROTTI (1968) considers *Cadulus olivii, C. strangulatus* and *C. tumidosus* doubtful species or mere variations of *C. ovulus*.

Table I. Scaphopoda reported from the Iberian coasts but not in present material. Asterisks mark doubtful species (see Discussion).
Tabla I. Escafópodos citados en las costas ibéricas pero no hallados en el presente material. Los asteríscos indican especies dudosas (ver Discusión)

Species	Area	Reference
Order DENTALIIDA		
Family DENTALIIDAE		
Antalis panorma (Chenu, 1842-47)	Mediterranean, Northeast Spain, Balearic Ils.	Locard, 1898; Hidalgo, 1917
Antalis rossati (Caprotti, 1966)	Mediterranean, Northeast Spain	Alzuria, 1986
Fissidentalium candidum (Jeffreys, 1877)	Biscay	Jeffreys, 1877
FUSTIARIIDAE		
Fustiaria rubescens (Deshayes, 1825)	Mediterranean	Locard, 1898; Hidalgo,
1917, Alzuria, 1987		
Order GADILIDA		
Suborder ENTALIMORPHA		
Family ENTALINIDAE		
Subfamily BATHOXIPHINAE		
Bathoxiphus ensiculus (Jeffreys, 1877)	Atlantic, Portugal, Biscay	Jeffreys, 1877
Subfamily HETEROSCHISMOINAE		
Heteroschismoides subterfissum	Atlantic, Portugal,	Locard, 1898
Suborder GADILIMORPHA		
Family GADILIDAE		
Subfamily SIPHONODENTALIINAE		
Siphonodentalium lobatum (Sowerby, 1860)	Atlantic, Portugal	Jeffreys, 1882
Subfamily GADILINAE		
Cadulus artatus Jeffreys, 1880	Atlantic, Biscay	Locard, 1898
Cadulus subfusiformis (M. Sars, 1865)	Atlantic, Biscay, Mediterranean	Locard, 1898; Monterosato, 1875
Cadulus gracilis Jeffreys, 1877	Biscay	Locard, 1898
Cadulus propinquus G. O. Sars, 1878	Biscay	Locard, 1898
Cadulus cylindratus Jeffreys, 1877	Biscay	Locard, 1898
Cadulus monterosatoi Locard, 1897	Atlantic, Galicia, Portugal	Locard, 1898
Cadulus gibbus Jeffreys, 1882	Biscay	Locard, 1898
Cadulus ovulus (Philippi, 1844)	Biscay, Mediterranean	Locard, 1898
Cadulus amphorus Jeffreys, 1882	Atlantic, South Portugal	Locard, 1898
**Cadulus olivii* (Scacchi, 1835)	Biscay	Jeffreys, 1882
**Cadulus tumidosus* Jeffreys, 1877	Atlantic, Biscay, Galicia, Southern Portugal	Locard, 1898
**Cadulus strangulatus* Locard, 1897	Biscay, Mediterranean off Marseilles	Locard, 1898

The occurrence of *C. subfusiformis,* a widespread Atlantic species, in the Mediterranean remains controversary. Although MONTEROSATO (1880) identifies a variation (var. *abyssicola*) from Palermo, CAPROTTI (1968) does not list this species as constant inhabitant of the Mediterranean. Recently, GAGLINI (1985) reconfirmed *C. subfusiformis,* and also MIFSUD's (1996) photograph of *C. jeffreysi* from Malta looks more like *subfusiformis*. However, until further reports come in, it remains possible that in the Mediterranean *C. subfusiformis* occurs in episodic pseudopopulations only (BOUCHET AND TAVIANI, 1992).

Long lists of synonyms as for some Mediterranean scaphopod species may have several reasons. One of them, espe-

cially when generic designations vary, is progress in supraspecific systematics. Another reason may be closely related but morphologically variable species and / or similar but not identical fossil forms. The species complex of *Antalis inaequicostata, novemcostata* and the Miocene *mutabile* (Doderlein in Hörnes, 1856) is a good example for a combination of these causes. *Antalis mutabile* and *A. inaequicostata* are very similar and both highly variable in their shell features. Bucquoy *et al.* (1886) recognize the close relationship of *mutabile* and *inaequicostata* (*=alternans*). Pilsbry and Sharp (1897-98) go further and list *mutabile* as synonym of both *dentalis* (p. 53) and *novemcostata* (p. 211). Ruggieri (1948) suggests *mutabile* being ancestral to *novemcostata*. Caprotti (1979) takes the alternative view and presents the recent *inaequicostata* as subspecies of the fossil *mutabile*. On the other hand, he assigns species status to *novemcostata*, although considering it the Atlantic descendant of *mutabile*. Finally, Pavia's (1991) questionable assignment of *mutabile* to the genus *Fissidentalium* leaves little doubt about its species status. In this case, there are two arguments for treating the presumed ancestor and the descendants as separate species. First, according to Caprotti (1979: 232), there is a "typical *mutabile*" to be distinguished from *inaequicostata*, the latter being extremely variable. Second, there is no fossil record of either species from the Tabianian (Lower Pliocene). Thus, there is a gap between the latest *mutabile* fossils from the Miocene and the earliest *inaequicostata* remains from the Middle Pliocene. This suggests that *mutabile* became extinct during the desiccation of the Mediterranean in the Upper Miocene (Rögl and Steininger, 1983, 1984), and *inaequicostata* radiated back into the Mediterranean Basin from the Atlantic, perhaps splitting from *novemcostata*, the possible sister species from the European southwest coasts. A study of the relationships of the recent European shallow water *Antalis* species with molecular techniques is needed to bring more clarity on this question.

That the re-colonisation of the Mediterranean by scaphopods around the Miocene-Pliocene transition is not necessarily connected with speciation is demonstrated by the cases of *A. dentalis* and *Entalina tetragona*. Both species are represented in the fossil record almost unchanged (Caprotti, 1965; 1968; 1979) from the Miocene on.

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Análisis parasitológico de gasterópodos acuáticos del delta del Llobregat (Barcelona). Estadios larvarios de trematodos digénidos

Parasitological study on aquatic gastropods from the Llobregat delta (Barcelona). Larval stages of digenetic trematodes

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RESUMEN

Se ha estudiado, durante los años 1990 a 1995, el índice de parasitación por estadios larvarios de trematodos digénidos de 6. 184 gasterópodos acuáticos recolectados en el delta del Llobregat, pertenecientes a 4 especies, 2 prosobranquios (Hydrobiidae) y 2 pulmonados (Ellobiidae, Physidae). El hidróbido *Mercuria confusa* (Frauenfeld, 1863) ha resultado ser el único parasitado por digénidos, mostrando una prevalencia de infestación del 3,22% (168 positivos sobre 5.219 analizados). Se han detectado hasta 5 especies de trematodos en estadio larvario, las cuales siguen dos modalidades de ciclo biológico: a) emisión de cercarias (xifidiocercarias Lecithodendriidae Odhner, 1910 y Microphallidae Travassos, 1920, cercarias inermes Notocotylidae Lühe, 1957; b) ausencia de emergencia cercariana (Microphallidae y Heterophyidae -Leiper, 1909- Odhner, 1914). La alta densidad poblacional de *M. confusa* y su susceptibilidad de ser parasitado por larvas de diversas especies de digénidos revelan su importancia en el mantenimiento de los ciclos biológicos de trematodos, ratificando el significativo papel que ejercen los prosobranquios como hospedadores intermediarios específicos en ambientes palustres.

ABSTRACT

Aquatic gastropods from the Llobregat delta were studied in order to detect infection prevalence by larval digenetic trematodes in the period 1990-1995. Specimens analysed (6.194) belonged to 4 species, 2 prosobranchs (Hydrobiidae) and 2 pulmonates (Ellobiidae, Physidae), the hydrobiid *M. confusa* (Frauenfeld, 1863) being the only infected. Larvae of 5 trematode species were detected following two life cycle modalities: a) cercarial emergence (xifidiocercariae Lecithodendriidae Odhner, 1910 and Microphallidae Travassos, 1920, unarmed cercariae Notocotylidae Lühe, 1957); b)without cercarial emergence (Microphallidae and Heterophyidae -Leiper, 1909- Odhner, 1914). The high density of *M. confusa* population and its susceptibility to infection by several digenetic species show it to be a specific intermediate host in the life cycle of these parasites, thus confirming the significant role of prosobranchs in the maintenance of trematode life cycles in deltaic zones.

PALABRAS CLAVE: delta del Llobregat, Prosobranchia, Hydrobiidae, *M. confusa*, estadios larvarios de digénidos, Lecithodendriidae, Microphallidae, Notocotylidae, Heterophyidae.
KEY WORDS: Llobregat delta, Prosobranchia, Hydrobiidae, *M. confusa*, larval stages of Digenea, Lecithodendriidae, Microphallidae, Notocotylidae, Heterophyidae.

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INTRODUCCIÓN

Las marismas del delta del Llobregat acogen una amplia variedad de gasterópodos acuáticos y terrestres, distribuidos en las lagunas, canales y terrenos colindantes, especies que se extienden por toda la planicie litoral en abundantes poblaciones y cuya distribución y frecuencia ha quedado reflejada en el estudio de ALTIMIRA (1969), autor que describe hasta 79 especies presentes en diversos hábitats deltaicos, destacando asimismo los tratados malacológicos generales elaborados por HAAS (1929), VIDAL ABARCA Y SUÁREZ (1985) y BECH (1990).

La importancia parasitológica de este grupo zoológico de invertebrados reside en el destacado papel que ostentan sus especies como primeros hospedadores intermediarios específicos, albergantes de esporocistos, redias y cercarias, de prácticamente todas las especies parásitas de trematodos digénidos de ciclos biológicos conocidos; pudiendo representar un doble papel en los ciclos abreviados, al intervenir como primeros y segundos hospedadores intermediarios simultáneamente, albergantes además de metacercarias.

El proceso natural de eutrofización existente en este tipo de ambiente lagunar, caracterizado por la presencia constante de agua salobre, rica en materia orgánica, y la descomposición de la vegetación helofítica, constituye el factor primordial para el asentamiento de moluscos eurihalinos. Otros pequeños invertebrados que conviven estrechamente con los anteriores (crustáceos e insectos) pueden actuar como segundos hospedadores intermediarios de estos digénidos, sirviendo, asimismo, como fuente de alimentación de la fauna vertebrada (aves, micromamíferos, peces), hospedadores de las formas adultas del parásito.

El conocimiento de la biología de los digénidos en este tipo de ambiente palustre requiere un seguimiento previo de las especies hospedadoras parasitadas, de los biotopos que frecuentan y de su comportamiento. En este sentido, cabe destacar los numerosos trabajos faunístico-ecológicos realizados en el delta del Ebro, basados en las especies vermidianas y sus hospedadores micromamíferos (FELIU, TORRES, GÁLLEGO, GOSÁLBEZ Y VENTURA, 1985; GRACENEA, FELIU, MONTOLIU, TORRES Y GÁLLEGO, 1987; FELIU, TORRES, GRACENEA Y MONTOLIU, 1990), trabajos que han servido como punto de referencia para el estudio de los ciclos biológicos, principalmente acuáticos, de digénidos que tienen lugar en dicho enclave (MONTOLIU, GRACENEA, VILLA Y GONZÁLEZ-MORENO, 1991). De la misma forma, los llevados a cabo en pequeños mamíferos del delta del Llobregat, menos numerosos y caracterizados por recoger una fauna parasitaria cualitativamente y cuantitativamente más pobre (GRACENEA Y MONTOLIU, 1992; GRACENEA, MONTOLIU Y DEBLOCK, 1993), han sido ampliados con el estudio parasitológico de diversas especies de moluscos, hospedadoras de larvas de digénidos tanto de ciclo acuático (MONTOLIU, GRACENEA Y DEBLOCK, 1992), como de ciclo terrestre (GONZÁLEZ-MORENO, GRACENEA, MONTOLIU Y VILLA, 1994). Continuando en esta línea de investigación sobre ciclos biológicos de trematodos parásitos, este trabajo muestra la diversidad existente en la helmintofauna larvaria asociada a gasterópodos acuáticos adaptados a hábitats deltaicos.

MATERIAL Y MÉTODOS

Recolección de caracoles y mantenimiento en el laboratorio: El enclave prospectado, ya señalado anteriormente por GONZÁLEZ-MORENO *ET AL.* (1994), comprende los márgenes de la laguna de La Ricarda (Biotopo A) y terrenos colindantes del margen derecho parcialmente inundados por las aguas (Biotopo B) (ver Figura 1). Ambos puntos de muestreo constituyen el hábitat de asentamiento de diversas comunidades de moluscos, especies que son capaces de soportar la intensa fluctuación estacio-

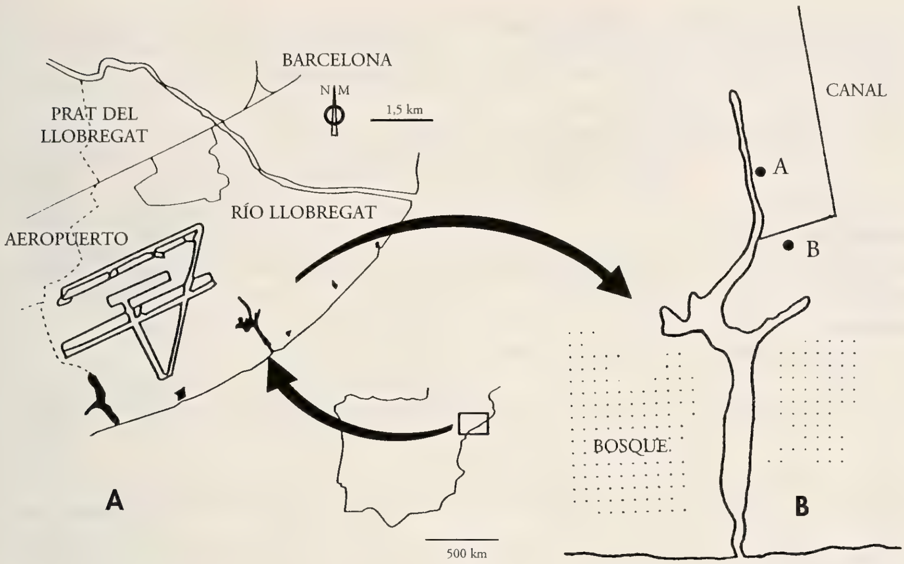

Figura 1. Situación geográfica de la zona prospectada en el delta del Llobregat. A: laguna de La Ricarda. B: localización de los biotopos estudiados.
Figure 1. Geographic situation of the prospected areas in the Llobregat delta. A: La Ricarda lagoon. B: localization of the study areas.

nal del enclave, con aporte constante de agua dulce procedente de los canales y del acuífero superficial e infiltración de agua marina.

Biotopo A: la vegetación natural predominante en esta comunidad helofítica son los cañizares que bordean el margen de la laguna, con una especie predominante, el cañizo (*Phragmites australis*), cuyos tallos parcialmente sumergidos permiten el ascenso de los gasterópodos hacia la superficie. Agua de salinidad variable (3-8‰)y pH entre 7 y 8.

Biotopo B: constituido por zonas anegadas, poco profundas, cercanas al margen derecho de la laguna, alimentadas esencialmente por los canales de desagüe y las lluvias; con predominio de la vegetación helofítica asociada a especies halófilas. Junto a las gramíneas (*Phragmites*) se encuentra la espadaña (*Typha angustifolia, T. latifolia*), el esparto (*Spartina juncea*), así como una comunidad bentónica (*Enteromorpha, Ulva, Chara*); dado el menor aporte de agua marina la salinidad es menor (2-5‰) y pH entre 7 y 8.

Las especies de caracoles recolectadas en ambas zonas de muestreo han sido seis: 2 prosobranquios, *Mercuria confusa* (Frauenfeld, 1863) y *Potamopyrgus jenkinsi* (Smith, 1889) (Hydrobiidae) y 2 pulmonados, *Ovatella* (*Myosotella*) *myosotis* (Draparnaud, 1801) (Ellobiidae) y *Physa acuta* (Draparnaud, 1805) (Physidae). En la Tabla I queda reflejado el número de caracoles de cada especie estudiado, el biotopo de prospección y la época de recolección.

El estudio ha abarcado un periodo de cinco años (1990-95) con muestreos en primavera y otoño. Para ello, fueron utilizados tamices metálicos con los que se procedía a barrer el fondo fangoso o bien se practicaban pequeñas sacudidas de las partes sumergidas de la vegetación acuática. Una vez en el laboratorio los moluscos eran estabulados, reproduciendo las características específicas de cada zona de captura: con una salinidad

Tabla I. Especies de gasterópodos estudiadas: distribución del número de ejemplares según época de recolección y biotopo prospectado (A, B).
Table I. Gastropod species analysed: specimen distribution in the prospected biotopes (A, B) and annual variation.

	1990	1991	1992	1993		1994		1995	Total
	A	A	A	A	B	A	B	B	
Prosobranchia									
Mercuria confusa	1215	656	271	989	708	146	1164	70	5219
Potamopyrgus jenkinsi	12	21	9	224	-	40	-	36	342
Pulmonata									
Ovatella (Myosotella) myosotis	25	6	17	36	-	-	-	-	84
Physa acuta	4	40	-	121	-	170	36	168	539

y pH adecuados, dieta constituída por lechuga seca y alimento para peces.

Detección y aislamiento de formas larvarias de digénidos: La detección de una posible emisión de cercarias al medio externo se efectuó disponiendo individualmente los gasterópodos en pocillos de placa de cultivo celular conteniendo agua del biotopo y observándolos posteriormente bajo la lupa en búsqueda de cercarias nadando libremente. Para la detección de esporocistos, redias y metacercarias, se procedió a la disección de los caracoles y a la observación de todos sus órganos.

Técnicas microscópicas: Las larvas fueron inicialmente estudiadas *in vivo* con el microscopio óptico y con la ayuda del colorante vital rojo neutro, procediéndose posteriormente a la fijación con el líquido de Bouin, tinción con carmín alumínico y tras cuidadosa deshidratación se montaron con Bálsamo del Canadá.

RESULTADOS

El estudio de 5.219 ejemplares de *M. confusa* ha puesto de manifiesto la capacidad de este prosobranquio, el único gasterópodo que ha resultado estar parasitado, para albergar diferentes formas larvarias de digénidos, en total cinco especies caracterizadas por su ciclo biológico acuático. Todas las infestaciones por digénidos han mostrado invasión a nivel del complejo glándula digestiva-gónada, como hábitat de elección para la evolución de las larvas.

Las especies de digénidos detectadas, pertenecientes a 4 familias, presentan dos modalidades de ciclos biológicos (Fig. 2). En la primera de ellas, es característica la emisión de cercarias al medio externo, bien sea en ciclos triheteroxenos (con tres hospedadores) o diheteroxenos (con dos hospedadores). En la segunda modalidad, ciclo de tipo abreviado, el gasterópodo se comporta como primer y segundo hospedador intermediario simultáneamente, no habiendo emisión de cercarias.

I. Emisión de cercarias

I. a. Ciclos triheteroxenos

Cercarias Lecithodendriidae. Lecithodendriidae gen. sp.: Cercarias xifidiocercas (con estilete), distomas, provistas de una cola recta más estrecha que el cuerpo (leptocercas) y virguladas (cuerpo: 150 x 90 μm). Originadas en esporocistos sacciformes (100-350 x 50-100 μm) provistos de poro de salida musculoso a través del cual las cercarias emergen según un patrón de emisión predominantemente nocturno.

La morfoanatomía de estas cercarias se ajusta a la descrita para la familia Lecithodendriidae (Yamaguti, 1975; Schell, 1985), destacando su afinidad con xifidiocercarias Lecithodendriidae

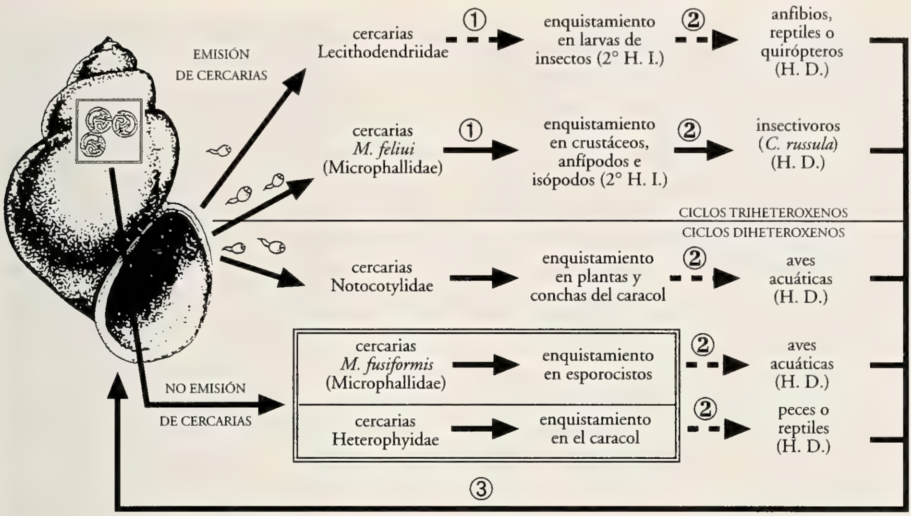

Figura 2. Ciclos biológicos de los digénidos detectados en *Mercuria confusa*. (—): fases conocidas. (- -): fases presumibles. 2° H. I.: segundo hospedador intermediario. H. D.: hospedador definitivo. 1: penetración activa. 2: penetración pasiva. 3: huevos en heces del H. D.
Figure 2. Life cycles of digeneans detected in Mercuria confusa. *(—): known phases. (- -): likely phases. 2° H. I.: second intermediate host. H. D.: definitive host. 1: active penetration. 2: pasive penetration. 3: eggs in definitive host feces.*

detectadas en otros biotopos deltaicos geográficamente próximos, el delta del Ebro (MONTOLIU *ET AL.*, 1991) y costa francesa mediterránea (DEBLOCK, 1980).

Las cercarias probablemente infestan larvas de insectos (segundos hospedadores intermediarios, en los que se forma la metacercaria), desarrollándose el adulto probablemente en anfibios y reptiles (LLUCH, ROCA Y NAVARRO, 1986) o en quirópteros (ESTEBAN, OLTRA-FERRERO, BOTELLA Y GRANEL, 1993) por depredación, aunque sin descartar su posible presencia en micromamíferos (GRACENEA *ET AL.*, 1987).

Cercarias Microphallidae. *Maritrema feliui* Gracenea, Montoliu et Deblock, 1993: Xifidiocercarias, monostomas, anentéricas y leptocercas (cuerpo: 120 x 68 μm), de fórmula excretora 2((2+2)+(2+2)= 16 solenocitos. Se originan en esporocistos de aspecto sacciforme e irregular, (166-430 x 140-180 μm), provistos de poro de salida. La emergencia cercariana se produce predominantemente en horas crepusculares.

La realización experimental del ciclo biológico, descrito sucintamente por los autores de la especie, ha permitido su determinación sistemática. Las cercarias infestan activamente a crustáceos anfípodos e isópodos (segundos intermediarios), evolucionando a metacercarias enquistadas, los cuales son depredados por el hospedador definitivo, el insectívoro *Crocidura russula* (Hermann, 1780) en el delta del Llobregat, en el que se originan los adultos a nivel intestinal (GRACENEA Y MONTOLIU, 1992; GRACENEA *ET AL.*, 1993).

I. b. Ciclos diheteroxenos

Cercarias Notocotylidae. Notocotylidae gen. sp.: Cercarias de gran tamaño (cuerpo: 600-800 μm x 370 μm) y gran opacidad, inermes (ausencia de estilete), oftalmocercas (con manchas oculares), monostomas y leptocercas. Se originan en redias de aspecto fusiforme, provis-

tas de faringe subterminal y ciego intestinal de gran volumen. Las cercarias acaban de madurar fuera de las redias, emergiendo al medio externo y enquistándose rápidamente en la vegetación o sobre la misma concha del caracol, evolucionando a metacercarias (cuerpo: 736 x 138 μm) confinadas en quistes hemiesféricos (diámetro, 150-300 μm).

La morfología de las cercarias y el ciclo diheteroxeno con enquistamiento en el medio acuático son propios de la familia Notocotylidae (Yamaguti, 1975; Schell, 1985). Los adultos se desarrollan presumiblemente en aves acuáticas deltaicas (hospedadores definitivos) al alimentarse éstos de plantas acuáticas o de moluscos.

II. No emisión de cercarias (ciclos abreviados)

Cercarias Microphallidae. *Microphallus fusiformis* Reimer, 1963: Cercarias rudimentarias (blastocercarias) de reducidas dimensiones (50-70 x 30-37 μm), inmóviles y constituidas por células indiferenciadas, sin apéndice caudal ni esbozos de otras estructuras. Se forman en esporocistos blanquecinos, transparentes (200-500 x 150 μm) y sacciformes, en los que evolucionan a metacercarias enquistadas (diámetro, 80-110 x 59-64 μm).

La metacercaria desenquistada se caracteriza por su pequeño tamaño (140-160 x 60 μm) y cuerpo fusiforme muy espinulado; de carácter progenético, con testículos y glándulas vitelógenas funcionales; ovario diestro y metratermo confluyendo a nivel de la pared lateral del atrio genital La morfología de dichas metacercarias, muy similar a la del adulto (Montoliu *et al.*, 1992). El hospedador definitivo en el delta lo constituyen probablemente aves anseriformes (Reimer, 1963).

Cercarias Heterophyidae. Heterophyidae gen. sp.: Cercarias monostomas, leptocercas y oceladas, con órgano de penetración protráctil (cuerpo: 100-120 x 50-60 μm) y sistema excretor provisto de glándula post-vesical. Evolucionan a partir de redias de aspecto cilíndrico (158-370 x 52-103 μm), provistas de faringe musculosa y un ciego corto. Las cercarias, tras emerger de la redia, se enquistan dentro del mismo caracol.

Las metacercarias están provistas de una doble corona de espinas rodeando a la boca. Son distomas, con testículos homolaterales, vesícula excretora de gran tamaño, encontrándose confinadas en quistes (80x70 μm) de doble cubierta. Las aves acuáticas, peces o anfibios podrían actuar como hospedadores definitivos del digénido (Yamaguti, 1975).

En la Tabla II se encuentran recopiladas las prevalencias de infestación en *Mercuria confusa* para cada una de las especies descritas anteriormente.

DISCUSIÓN

Los estudios sobre la helmintofauna larvaria de digénidos de ciclo acuático señalan a los moluscos prosobranquios como los principales hospedadores intermediarios específicos para las especies Digenea de ambientes palustres. Los datos obtenidos en nuestro estudio han mostrado que el hidróbido *Mercuria confusa* interviene como hospedador intermediario específico de cinco especies de digénidos deltaicos. Este prosobranquio ha sido estudiado parasitoló-

(Página derecha). Figura 3. Estadios larvarios de digénidos detectados en *Mercuria confusa*. A: cercaria Lecithodendriidae (rojo neutro). B: blastocercaria y quistes metacercarianos intrasporocísticos de *M. fusiformis*. C: metacercaria enquistada Heterophyidae. D: cercaria de *M. feliui* (rojo neutro). Escalas 25 µm.

(Right page). Figure 3. Digenean larval stages detected in Mercuria confusa. *A: cercaria Lecithodendriidae (neutral red). B: intrasporocystic blastocercaria and metacercarial cysts of* M. fusiformis. *C: encysted metacercaria Heterophyidae. D: cercaria of* M. feliui *(neutral red). Scale bars 25 µm.*

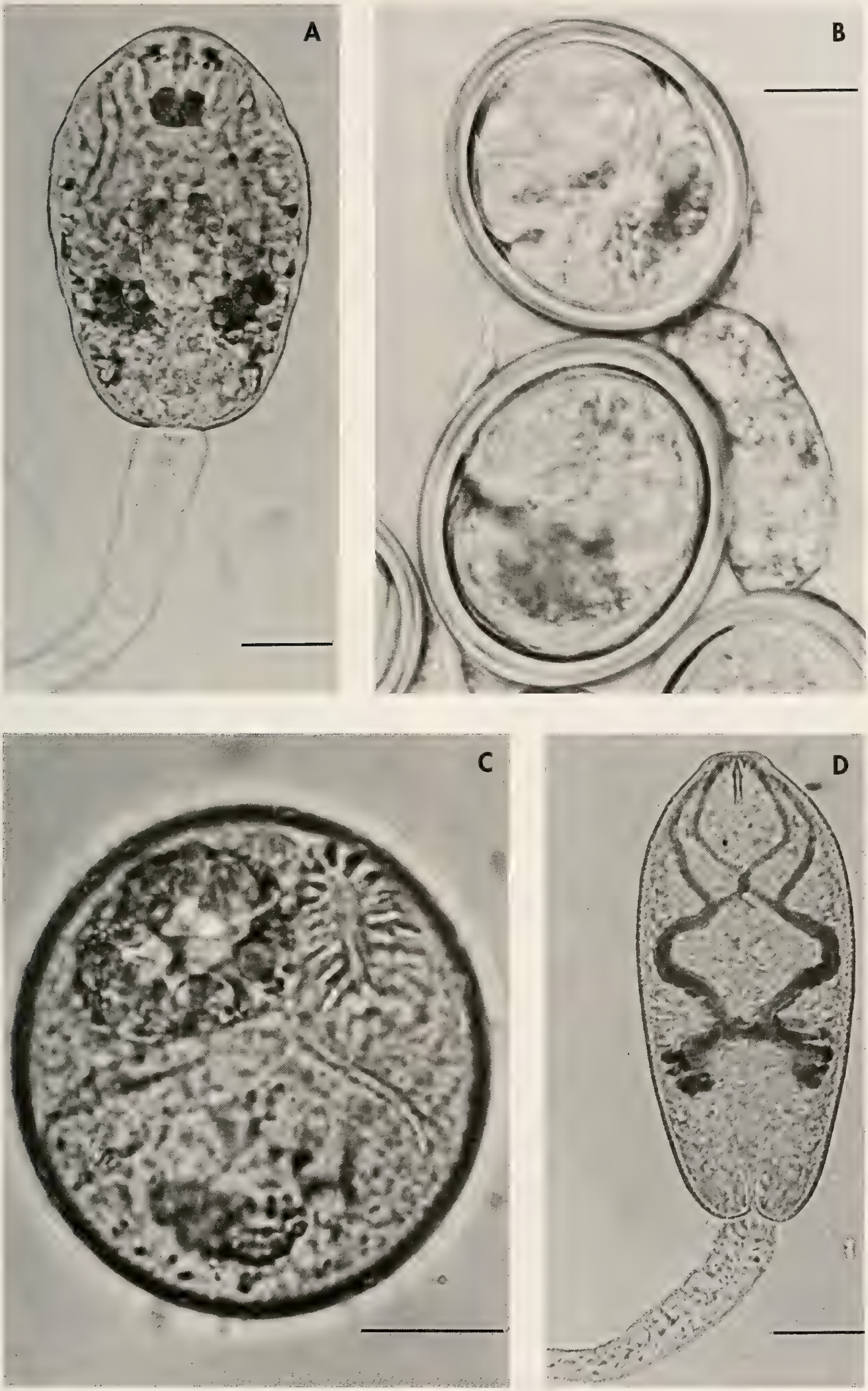
A
B
C
D

Tabla II. Parasitación de *M. confusa* por estadios larvarios de digénidos según épocas de recolección y biotopo prospectado (A, B). N=nº de especímenes estudiados (por emisión y/o por disección). %=prevalencia de parasitación.

Table II. Infection of M. confusa *with larvae of digenetic trematodes, related to year of collection and prospected biotopes (A, B). N=number of examined snails (emergence and/or dissection). %=prevalence of infection.*

	1990	1991	1992	1993		1994		1995	Total
	A	A	A	A	B	A	B	B	
	%	%	%	%	%	%	%	%	%
Cercarias+Esporocistos (o redias) (emisores de cercarias)									
	N=1215	N=656	N=271	N=989	N=708	N=146	N=1164	N=70	N=5219
Lecithodendriidae gen sp.	-	-	-	0,40	0,42	-	0,28	-	0,15
Maritrema feliui	1,97	3,35	4,43	0,42	0,14	-	1,37	4,29	1,76
Notocotylidae gen. sp.	-	0,30	0,37	-	-	-	0,17	-	0,10
Cercarias+Esporocistos (o redias) + metacercarias (ciclos abreviados)									
	N=492	N=482	N=33	N=475	N=210	N=32	N=150	N=0	N=1874
Microphallus fusiformis	7,52	2,07	-	-	-	-	-	-	2,51
Heterophyidae gen. sp.	3,25	-	-	-	-	-	-	-	0,85

gicamente con anterioridad en el delta del Ebro por MONTOLIU *ET AL.* (1991), detectándose formas larvarias pertenecientes a 7 especies de digénidos. La ausencia de parasitación en el prosobranquio *Potamopyrgus jenkinsi*, en el que sólo han sido estudiadas hembras partenogenéticas, podría deberse a un fenómeno similar al observado por LIVELY (1989) para otras especies de *Potamopyrgus* Stimpson, 1865 en Nueva Zelanda, en las que se demuestra la correlación positiva entre las poblaciones sexuadas y la parasitación por microfálidos, no estando nunca parasitadas las poblaciones que se reproducen exclusivamente por partenogénesis. En lo que respecta a las especies de pulmonados estudiadas, si bien éstas no se encuentraron parasitadas por digénidos, sí que existen numerosas citas de infestaciones por otras especies de digénidos en ejemplares dulceacuícolas europeos (MOUAHID Y MONÉ, 1988, entre otras).

La prevalencia de parasitación por larvas de digénidos mas alta detectada en *M. confusa* ha correspondido a la familia Microphallidae. Los digénidos de biología conocida de esta familia incluyen a diversos moluscos prosobranquios como hospedadores intermediarios, tanto en las especies triheteroxenas como las diheteroxenas, de ciclo abreviado. En la primera modalidad, para las especies de *Maritrema* Nicoll, 1907 y *Microphallus* Ward, 1901, son los prosobranquios pertenecientes a *Littorina* Ferrusac 1822 (BENJAMIN Y JAMES, 1987; IRWIN, MAGUIRE Y SAVILLE, 1990; GALAKTIONOV Y BUSTNERS, 1995) y a *Hydrobia* Hartmann, 1821 (GARKAVI, 1972; PREVOT Y BARTOLI, 1977; DEBLOCK, 1978; SAVILLE Y IRWIN, 1991) los más frecuentemente citados, y más puntualmente los prosobranquios *Bythinella* Moquin-Tandon, 1855 (JOURDANE, 1979), *Pseudamnicola* Paulucci, 1878 (KULKINA Y BELYAKOVA, 1983), *Cerithium* Bruguière, 1789, *Bittium* Leach, 1847 (PREVOT, BARTOLI Y DEBLOCK, 1976; BARTOLI Y PREVOT, 1978) y *Cerithidea* Swainson, 1840 (ABDUL-SALAM Y SREELATHA, 1991). El género *Microphallus* es el que engloba el mayor número de especies con ciclos abreviados, interviniendo habitualmente especies de *Hydrobia* y *Littorina* y puntualmente de *Bittium*, incluyéndose únicamente a especies de *Hydrobia* para el género *Maritrema* (DEBLOCK, 1977; LAUCKNER, 1984).

En lo que se refiere a la familia Lecithodendriidae, los prosobranquios vuel-

ven a ser citados frecuentemente en los trabajos sobre trematodofauna larvaria, destacando los realizados en especies de *Bithynia* Leach, 1818 (YAMAGUTI, 1975) y *Amnicola* Gould y Haldemann, 1841 (CABLE, 1985). Con respecto a los hospedadores intermediarios de notocotílidos, cabe señalar a los prosobranquios *Hydrobia* (STUNKARD, 1966; DEBLOCK, 1980), *Potamopyrgus* (BISSET, 1977), *Bithynia* (YAMAGUTI, 1975; VASILEV Y KANEV, 1984), *Littorina* (GRANOVICH, MIKHALOVA Y SERGIEVSKII, 1987), así como a especies de melaníidos (KHALIFA Y EL-NAFFAR, 1979). En los digénidos heterófidos no son frecuentes los ciclos abreviados como el que tiene lugar en el delta del Llobregat, habiéndose citado a una sola especie de digénido, *Metagonimoides oregonensis* Price, 1931, la cual infesta a diversas especies de prosobranquios pleurocéridos, únicos hospedadores intermediarios del ciclo (YAMAGUTI, 1975).

El análisis cuantitativo de la parasitación por larvas de *M. confusa* muestra diferencias en las prevalencias para cada una de las especies de digénidos hallados (Tabla II). Los índices totales más elevados mostrados por los microfálidos (*Maritrema feliui* - 1,76 %; *Microphallus fusiformis* - 2,51 %) parecen ajustarse a los detectados en hidróbidos que habitan zonas geográficas litorales próximas al delta del Llobregat. MONTOLIU ET AL. (1991) muestran para *M. confusa* en el delta del Ebro unos niveles de parasitación para *Maritrema* sp. (1,36 %) muy similares a las del presente trabajo. Asimismo, en el estudio realizado por DEBLOCK (1978) se observan índices de parasitación por microfálidos en especies de *Hydrobia* que oscilan entre el 2,5 y 0,5% en el litoral atlántico y entre el 6 y 0,5% en el litoral mediterráneo. En otros prosobranquios litorales también muy estudiados del género *Littorina*, la prevalencia de estadios larvarios Microphallidae es muy alta, del orden del 23,8% en la costa del Mar Báltico (LAUCKNER, 1984) y de hasta el 40-50% en las costas soviéticas (SERGIEVSKII, 1985).

La baja prevalencia por lecitodéndridos en el Llobregat no parece ajustarse a las tasas de infestación observadas en *M. confusa* del delta del Ebro, en el que se alcanzan índices elevados (5,83%) (datos no publicados). Los bajos índices de infestación detectados en el resto de digénidos sí parecen coincidir con los obtenidos para este hidróbido en el Ebro, detectándose el 0,27% para cercarias Heterophyidae y el 0,20% para cercarias Notocotylidae, y con los de DEBLOCK (1978) en las costas francesas para especies de *Hydrobia*, 0,07-1,67% para heterófidos y 0,20-0,43% para notocotílidos.

En cuanto a la dinámica del parasitismo, las fluctuaciones temporales observadas en el hidróbido no parecen guardar relación directa con su densidad poblacional, relativamente constante en todas las prospecciones realizadas, o con el biotopo de prospección. Ello podría estar relacionado con el comportamiento de los hospedadores definitivos como factor de máxima influencia en dichas variaciones. *Maritrema feliui* es la única especie de digénido que parece mantenerse relativamente constante en el tiempo, hecho que puede explicarse por la presencia regular del insectívoro *Crocidura russula* en el delta (GRACENEA Y MONTOLIU, 1992). En cuanto a Notocotylidae gen. sp. y *Microphallus fusiformis*, potencialmente parásitos de aves deltaicas, su aparición más esporádica en los caracoles estaría condicionada por el carácter migratorio de sus hospedadores definitivos.

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On a floating egg mass of the diamond shaped squid *Thysanoteuthis rhombus* (Cephalopoda: Thysanoteuthidae) in the western Mediterranean

Observaciones sobre una puesta pelágica del calamar losange *Thysanoteuthis rhombus* (Cephalopoda, Thysanoteuthidae) hallada en el Mediterráneo occidental

Angel GUERRA and Francisco ROCHA*

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ABSTRACT

This is the second record of a floating egg mass of the diamond shaped squid *Thysanoteuthis rhombus* in the Mediterranean (37° 11.85′ N - 1° 31.15′ E). The first one was observed at the Strait of Messina in 1929. The egg mass was a dense, resilient oblong cylinder with rounded tips appoximately 100 cm in length and about 20 cm in diameter. From a small sample, egg capsules and paralarvae (1.85±0.08 mm ML) are described. Some complementary characters about this species paralarvae, such as the arm formulae, the presence of an incipient swimming keel-like shaped membrane on some arms, and the mantle chromatophore pattern should assist in their identification.

RESUMEN

En este trabajo se informa sobre el segundo hallazgo de una puesta pelágica del calamar losange *Thysanoteuthis rhombus* en el Mar Mediterráneo (37° 11,85′ N - 1° 31,15′ E). La primera se observó en el estrecho de Mesina en 1929. La masa de huevos consistía en un cilindro oblongo con los bordes romos, denso y elástico, de unos 100 cm de longitud y 20 cm de diámetro. A partir de una muestra pequeña que se pudo obtener se describen las cápsulas ovigeras y las paralarvas (1,85±0,08 mm ML). Se proporcionan algunos caracteres complementarios útiles para la identificación de estas paralarvas: la formula braquial, la presencia de una carena natatoria incipiente aquillada en algunos brazos y el patrón de cromatóforos en el manto.

KEY WORDS: Cephalopoda, *Thysanoteuthis rhombus*, egg mass, paralarvae, Mediterranean Sea.
PALABRAS CLAVE: Cephalopoda, *Thysanoteuthis rhombus*, puesta, paralarvas, mar Mediterráneo.

INTRODUCTION

The diamond shaped squid *Thysanoteuthis rhombus* Troschel, 1857 is an epipelagic inhabitant of warm tropical and partially subtropical waters of the World Ocean including the Mediterranean, often occurring in pairs or small schools

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(NISHIMURA, 1966; CLARKE, 1966; NIGMATULLIN, ARKHIPKIN AND SABIROV, 1995). It is a large oegopsid squid which reaches up to 85 cm in mantle length (ML) and 24 kg in body weight (NIGMATULLIN *ET AL.*, 1995). *T. rhombus* is one of the fastest-growing squid: in approximately one year, it reaches its maximum ML (NIGMATULLIN *ET AL.*, 1995). This species has high potential fecundity (up to 4.8 million oocytes), but a rather small maximum volume of oviducts (up to 140,000 eggs) and egg masses (35,000 to 75,000), which suggest that *T. rhombus* is an intermittent spawner with multiple filling and evacuation of oviducts (NIGMATULLIN *ET AL.*, 1991; NIGMATULLIN *ET AL.*, 1995).

T. rhombus is one of the few oegopsid cephalopods in which the spawn is known. Until recently, a total of 21 egg masses had been observed. All were found drifting in the surface water layer of the tropical Atlantic, northwest and southeast Pacific and the Mediterranean (review in SABIROV, ARKHIPKIN, TSYGANKOV AND SHCHETINNIKOV, 1987). Egg masses of this species are gelatinous, sausage-shaped, 60-180 cm long by 10-30 cm diameter; containing a double spirally arranged row of eggs embedded in the surface layer of the mass (MISAKI AND OKUTANI, 1976; SUZUKI, MISAKI AND OKUTANI, 1979). The egg mass was photographed in natural environment for the first time by SUZUKI *ET AL.* (1979). The first and unique reference to an egg mass of *T. rhombus* in the Mediterranean (Strait of Messina) was given by SANZO (1929).

Although the occurrence of this species in the Mediterranean is rare (MORALES, 1981; BIAGI, 1982; MANGOLD AND BOLETZKY, 1988) it seems that its presence is increasingly frequent as by-catch in some pelagic fisheries, particularly near the coast (EZZEDDINE-NAJAI, 1996). A pair of animals, male and female, were observed by divers in a submarine cave off the coast of Almeria (Southeast Spain) relatively near the place where the sample reported in this paper was collected (GUERRA, 1992).

This paper deals with the second record of the egg mass of *T. rhombus* in the Mediterranean after 67 years. A description of the planktonic paralarvae is given, emphasising several characteristics which may be used to identify the early stages of the species.

MATERIAL AND METHODS

The egg mass was discovered by the vessel "*Toftevaag*" at 08.27 h on August 27, 1995, at 37° 11.85′ N - 1° 31.15′ E in the western Mediterranean (Fig. 1). The reported egg mass was accompanied by other drifted pleuston, such as jelly-fish. The whole mass was so loose that it could not be taken out of the water. But a sample of gelatinous material containing 2 eggs in early stage of development, 1 embryo within its egg capsule, 2 paralarvae within the egg capsules, and 32 practically fully developed paralarvae outside the egg capsules were caught. This sample was fixed in 5% formalin. The identification was made based on the paralarvae which, although still embedded in the external gelatinous mass, were near hatching. These paralarvae have similar characteristics to those reported by STEPHEN (1992). Egg diameter, dorsal mantle length (ML) and total length (TL) of each paralarvae were measured using a dissecting microscope fitted with an eye-piece graticule.

RESULTS

The egg mass was a dense, resilient, oblong cylinder with rounded ends (Fig. 2A). The size of the whole mass was about 100 cm in length and about 20 cm in diameter. It was observed that the purple egg capsules lay in two rows, spirally arranged around the cylinder. The diameter of the egg capsules with the well developed embryo ranged from 2.8 to 3.0 mm. The average ML of paralarvae was 1.85±0.08 mm (n= 30) and its TL varied between 2.50 and 2.75 mm.

All paralarvae observed had the head inside the mantle cavity, only showing the arms and tentacles exter-

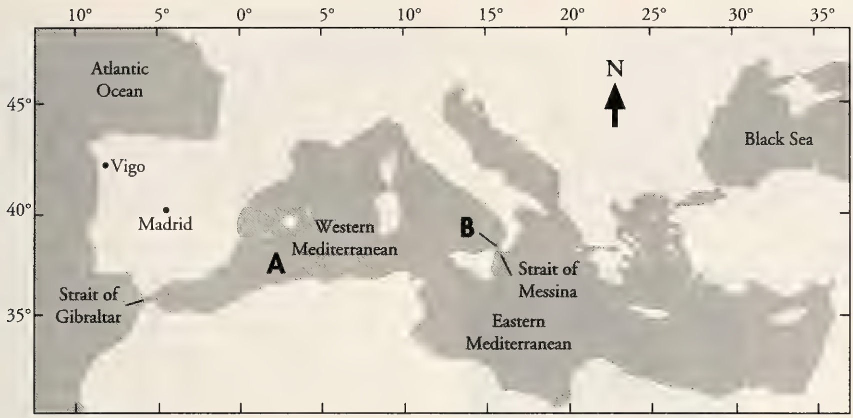

Figure 1. *Thysanoteuthis rhombus.* Location of the two floating egg masses collected in the Mediterranean Sea. A: This paper; B: SANZO (1929).
Figura 1. Thysanoteuthis rhombus. *Localización geográfica de las dos puestas pelágicas encontradas en el Mar Mediterráneo. A: Presente estudio; B: SANZO (1929).*

nally (Fig. 2B). The mantle is oval, stout, short and blunt posteriorly. The anterior margin of the mantle curves inwards in both dorsal and ventral sides, but is more pronounced ventrally. This may be a result of the preservation process which could had produced the retraction of the head inside the mantle cavity. The fins are subterminal, small and rounded; the fin length 19.5% ML (Figs. 2C, D). The paralarvae have broadly separated, slightly protruding eyes, and funnel locking cartilage (Fig. 2E) with a short, broad, transverse groove and a long, relatively wide, longitudinal groove (sideways ⊦shaped). The tentacles are short (about 33% of the ML), stouter and slightly longer than the longest arm (III); the I and IV pairs of arms are rudimentaries. Brachial formulae III>II>I=IV. Both, tentacles and developed arms, with small suckers, probably arranged in two rows. On arms II and III, an incipient swimming keel-like shaped membrane was present. Trabeculate protective membrane was absent in arms and tentacles.

The paralarvae show two types of chromatophores: a) large and pale-ochre chromatophores densely concentrated on dorsal, lateral and ventral mantle sides; and b) small, subtriangular dark-red chromatophores arranged in a single row around the anterior margin of the mantle. There is a light area between both types of chromatophores. Slight chromatophores were observed on the dorsal and ventral sides of the head, the tentacles and the arms. The fins lacked chromatophores.

DISCUSSION

The egg mass reported was captured near the surface in a zone were the inflow of Atlantic water into the Mediterranean is high due to the proximity of the Strait of Gibraltar. The water movements through this bottleneck are governed by an inflow of surface water into the Mediterranean, and a countercurrent of lesser volume carrying water of higher salinity into the Atlantic (MANGOLD AND BOLETZKY, 1988). The egg mass collected by SANZO (1929) was in the Strait of Messina where there are strong currents. Elsewhere egg masses of *Thysanoteuthis rhombus* occurred in regions with strong warm currents such as Kuroshio, Perú countercurrent and the Equatorial countercurrent (YAMAMOTO

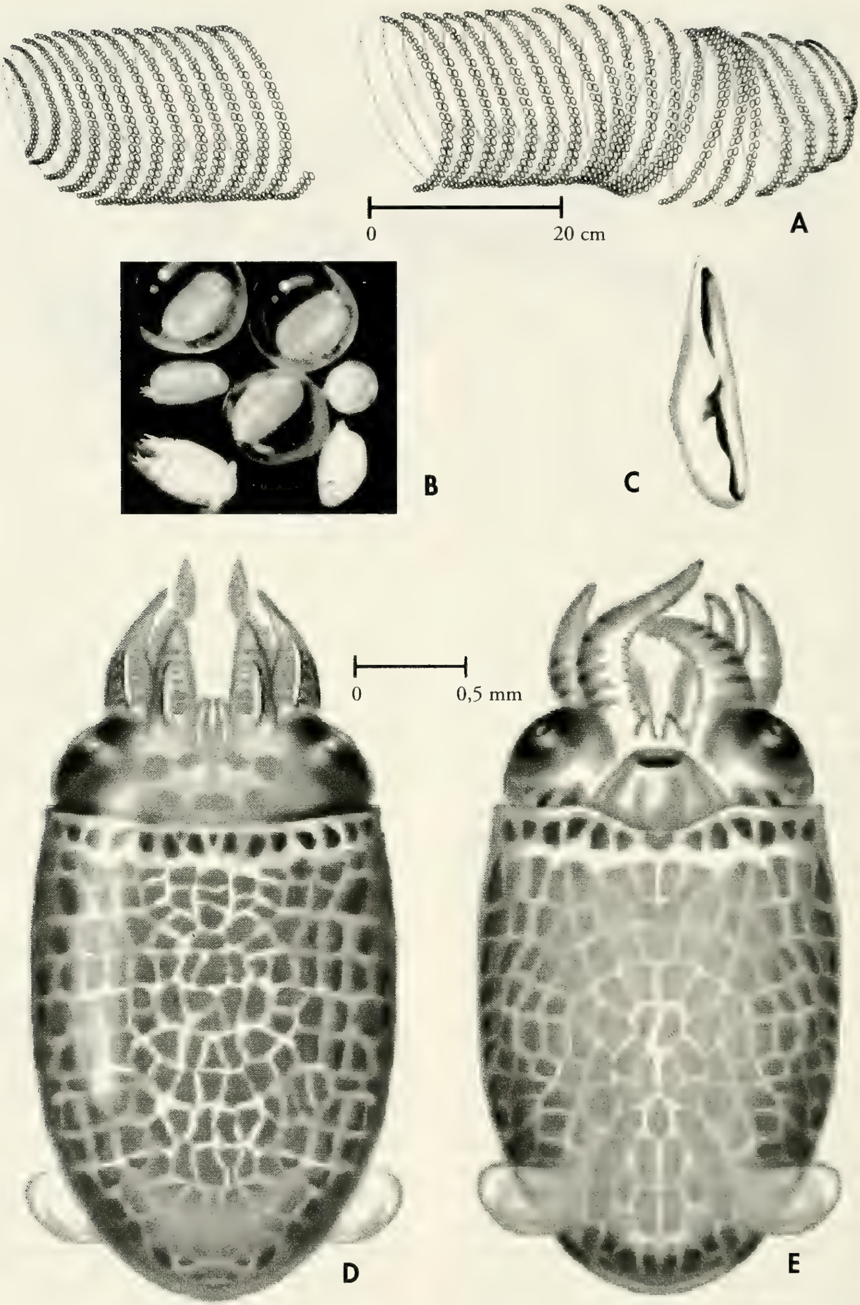

Figure 2. *Thysanoteuthis rhombus.* Floating egg mass and paralarvae. A: egg mass; B: Egg with non-developed embryo and paralarvae within the egg capsule; C: Funnel locking-cartilage of a newly hatched, 1.85 mm ML; D: Dorsal view of a newly hatched, 1.85 mm ML; E: Ventral view of the same specimen.
Figura 2. Thysanoteuthis rhombus. *Puesta pelágica y paralarva. A: Puesta pelágica; B: Huevo con embrión muy poco desarrollado y paralarva dentro de la cápsula ovígera; C: Cartílago de cierre en el sifón de un recién nacido de 1,85 mm ML; D: Visión dorsal de un recién nacido de 1,85 mm ML; E: Visión ventral del mismo ejemplar.*

AND OKUTANI, 1975; NIGMATULLIN *ET AL.*, 1995). Therefore, as in the Atlantic and the Pacific Oceans, in the Mediterranean the species seems to spawn in waters with strong currents.

NIGMATULLIN *ET AL.* (1995) indicated that *T. rhombus* spawns throughout the year in tropical waters, but during the warm season (summer and early autumn) in peripheral regions such as in the Mediterranean, which agree with the date when the egg mass reported was observed.

The egg mass in the report had a shape and a size which coincide with those given for the other egg masses illustrated (SANZO, 1929; MISAKI AND OKUTANI, 1976) and photographed (SUZUKI *ET AL.*, 1979).

Considering the dimension of this egg mass, the diameter of the egg capsules measured and calculating the surface of the egg mass as a cylinder (6,280 cm^2), an estimation gives a figure of about 66,800 eggs. This amount coincides with the total number of eggs in each egg mass calculated by SABIROV *ET AL.* (1987) which ranged from 32,000 to 76,000 eggs.

The embryo and paralarvae found have sizes, shapes and characters which largely coincide with those reported by ISSEL (1920), SANZO (1929) YAMAMOTO AND OKUTANI (1975) and MISAKI AND OKUTANI (1976) and summarised by CLARKE (1966) and STEPHEN (1992). Some complementary information about this species paralarvae, such as the arm formulae, the presence of an incipient swimming keel-like membrane on some arms, and the mantle chromatophore pattern should assist in their identification.

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Ontogenetic variation of statolith shape in the short-finned squid *Illex coindetii* (Mollusca, Cephalopoda)

Variacion ontogénica del estatolito de la pota *Illex coindetii* (Mollusca, Cephalopoda)

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ABSTRACT

Changes in statolith morphology of *Illex coindetii* are described from specimens ranging from 42 to 379 mm mantle length obtained during trawling activities in the North-eastern Atlantic. The growth of the statolith was differentiated in five developmental stages. It has been observed that the wing of the statolith has two different growth patterns, from the ventral zone to the dorsal one and viceversa. The rostral angle of the statolith varied during its ontogenetic growth from an obtuse angle to a 90° angle. The dorsal zone of the statolith is here named as dorsal dome, and the lateral and ventral zone the lateral dome.

RESUMEN

En este trabajo se describen los cambios en la morfología del estatolito de *Illex coindetii*. El estudio se llevo a cabo mediante el análisis de 341 ejemplares con longitudes del manto comprendidas entre 42 y 379 mm. Estos animales se capturaron en la pesquería de arrastre desarrollada en el Atlántico noreste. El crecimiento del estatolito fue diferenciado en cinco estadíos de desarrollo. Se observaron dos patrones diferentes de crecimiento del ala del estatolito, desde la parte ventral a la dorsal y viceversa. El angulo rostral varía en el crecimiento ontogénico del animal, desde un ángulo marcadamente obtuso a un ángulo recto. El crecimiento en longitud máxima y en anchura del estatolito se enlentece al llegar a la maduración de los animales. Se propone una variación en la nomenclatura del estatolito de esta especie.

KEY WORDS: *Illex coindetii*, statolith, morphology, North-eastern Atlantic.
PALABRAS CLAVE: *Illex coindetii*, estatolito, morfología, Atlántico noreste.

INTRODUCTION

Cephalopods play an important role in the trophic web of marine ecosystems as both predators and prey of many marine species (AMARATUNGA, 1983). These marine molluscs have been cited as components of the diet of such top predators as marine mammals (XAMPENY AND FILELLA, 1976; CLARKE, 1980, 1986; CLARKE, MARTINS AND PRINCE, 1993; GONZÁLEZ, LÓPEZ, GUERRA AND BA-

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RREIRO, 1994), large teleosteans (BOUXIN AND LEGENDRE, 1936; BELLO, 1991; GUERRA, SIMÓN AND GONZÁLEZ, 1993; CLARKE, CLARKE, MARTINS AND SILVA, 1995), sea-birds (RODHOUSE, CLARKE AND MURRAY 1987; CLARKE, CROAXALL AND PRINCE, 1991; FURNESS, 1994; CROAXALL AND PRINCE, 1996) and cephalopods (RASERO, GONZÁLEZ, CASTRO AND GUERRA, 1996, RODHOUSE AND NIGMATULLIN, 1996). Beaks, statoliths, chitinous sucker rings and, to a lesser extent, gladius, were the main structures which allowed a positive identification to the taxonomic level of species in studies about trophic relationships between cephalopods and other marine animals. These hard structures remain unaltered in the stomach contents of their predators and represent an important source of information on the trophic relationships where these animals are involved.

Statoliths of cephalopods are small hard paired structures composed by calcium carbonate in the form of aragonite. They are situated in fluid-filled cavities termed statocysts inside the cartilaginous skulls of the cephalopods belonging to the subclass Coleoidea (CLARKE AND MADDOCK, 1988a). The statolith and the macula (statoconia system) constitute the receptor organ for detection of gravity. This is one of the functions of the statocysts, in which the level of sophistication is equivalent to the vertebrate vestibular system (YOUNG, 1960, 1989; STEPHEN AND YOUNG, 1982; BUDELMANN, 1978, 1988, 1990).

Statoliths are also the structures most frequently used for studies on age and growth. The statoliths of many cephalopod species show growth increments, which have been shown to have a daily periodicity of deposition in several species (see JACKSON, 1994).

Since teuthoid statoliths are apparently species-characteristic and have a greater likelihood of fossilisation than other cephalopod structures, they have become very important for identification of fossil species (CLARKE AND FITCH, 1975, 1979). The applications of image analysis which have been used in the morphological study of the statoliths, both recent and fossil, have shed light on certain phylogenetic relationships among cephalopods (CLARKE AND MADDOCK, 1988a; 1988b). As was done with shape analysis of fish otoliths (CAMPANA AND CASSELMAN, 1993), the statolith morphology of cephalopods has been used also for stock discrimination (BORGES, 1995).

As ontogenetic changes do exist in the statolith (MORRIS AND ALDRICH, 1984; GUERRA AND SÁNCHEZ, 1985; CLARKE AND MADDOCK, 1988b; BRUNETTI AND IVANOVIC, 1991), some remains on the reliability of this approach about this subject. From descriptions based solely on one statolith from one specimen, the result of the analysis of shape can be altered (LOMBARTE, SÁNCHEZ AND MORALES-NÍN, 1995) and a correct prey identification could also be uncertain.

The aim of this study was to determine the changes in the statolith shape for the ommastrephid squid *Illex coindetii* (Vérany, 1839) during its ontogenetic growth.

MATERIALS AND METHODS

341 specimens of *Illex coindetii* were collected in the North-eastern Atlantic (Fig. 1) from November 1991 to October 1992. Fishing was carried out at depths ranging from 100 and 350 m over the Galician continental shelf. The animals were sexed, measured to the nearest mm mantle length (ML), weighed (to 0.1 g) and assigned a maturity stage according to LIPINSKI (1979). The squid ranged from 48 to 379 mm ML. The statoliths were removed from the head and preserved in 96% ethanol. Statolith major axis and maximum width were recorded. Then, the statoliths were measured using an eyepiece graticule. Terms used in descriptions were assigned following the nomenclature established by CLARKE (1978).

Measurements were made using an image analysis system (IAS); the equipment used is reviewed by MACY (1995). The description of the each develop-

Figure 1. *Illex coindetii.* Fishing area where the samples were obtained.
Figura 1. Illex coindetii. Area de pesca donde se obtuvieron las muestras.

mental stage of the statolith was made based on microphotographs.

RESULTS

Statolith morphology: Statolith maximum length ranged from 0.47 (female of 48 mm ML) to 1.66 mm (female of 360 mm ML). No significant differences ($p<0.05$) between maximum length and maximum width of male and female statoliths of equivalent ML were found at any stage of development. Therefore, sex does not affect the growth of the statolith in *Illex coindetii.*

Figure 2 shows a diagrammatic picture of the different parts of an adult *Illex coindetii* statolith in posterior and anterior view. Terms used in descriptions and the measurements made are also shown. Some characteristic features were observed in these statoliths: a) there is continuity between the dorsal dome and the lateral dome. This feature can be observed between the superior and inferior lobes of the lateral dome as well; b) the posterior dome groove is very patent; c) the rostrum is short and an anterior rostral lobe does not exist; d) the wing is very broad; e) the medial fissure is well developed and also has a small posterior indentation; f) the dorsal spur is very clear.

Statolith development: Although the above description refers to a late developmental stage of the statolith in an adult animal, the way to reach this definitive stage is quite complex. Thus, the statolith has become increasingly complex and passed through different stages which implies growth in different planes. These stages can be described as follows (Fig. 3):

Stage I: Statoliths of immature animals ranging from 50 to 80 mm ML. The medial fissure is not yet visible but will be situated under the dorsal dome. This area will be the surface where the wing will connect with the body of the

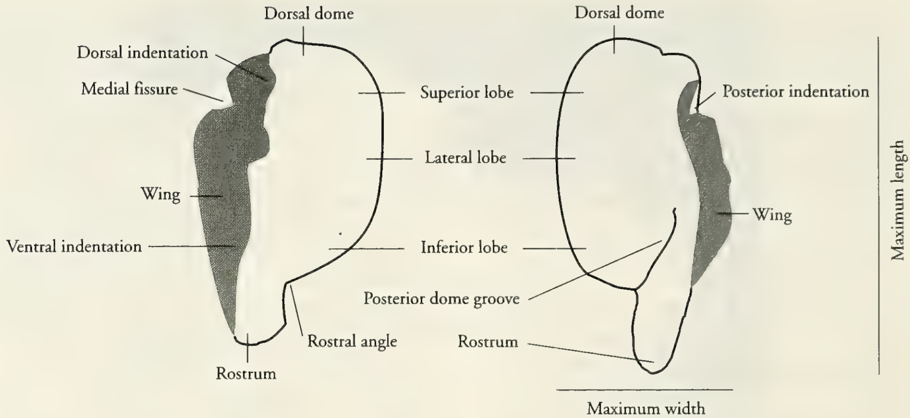

Figure 2. Diagrammatic picture of the different parts of an adult *Illex coindetii* statolith.
Figura 2. Diferentes partes del estatolito de un Illex coindetii *adulto.*

statolith in a later developmental stage. Another characteristic of the stage I statolith is the wide rostral angle (>140°). The primordium of the rostrum is also visible in the ventral zone of the statolith. It is virtually impossible to differentiate the dorsal dome, the superior and inferior lobes of the lateral dome, being round the general shape.

Stage II: This developmental stage includes the statoliths of animals with ML between 90 and 130 mm. The main characteristic of this stage is the growth of the rostrum, and the change in shape of the statolith, which is enlarging the ventral direction. Small dark zones in the ventral zone can be distinguished. This crystallisation will form the wing of the statolith. The wing formation is observed in two directions, from the rostrum to the dorsal plane of the statolith and from the dorsal dome to the ventral plane. There is a slight differentiation between superior and medium lateral dome.

Stage III: This stage is remarkably different from the preceding one. It appears in submature and mature squid ranging from 130 to 200 mm ML. The enlargement of the rostrum continues and the formation of the wing spans from the ventral to the dorsal zone. The medial fissure is small. A zone devoid of crystallisation called the foramen appears for the first time. The foramen runs parallel to the rostrum and will disappear gradually. The rostral angle is getting narrow and at this stage it forms almost a 90° angle.

Stage IV: Mature animals between 200 and 250 mm ML. The developmental stage is close to definitive conditions. The foramen is partially or totally occluded and the wing is formed along the entire statolith. As the statolith grows, the lobes become more distinct. Practically, the rostral angle is 90°.

Stage V: This stage describes the statoliths of mature specimens bigger than 250 mm ML. There are only minor changes in morphology from stage IV. Crystallisation in the wing is stronger and the foramen is totally occluded. The formation of the wing emphasises the medial fissure.

Figure 4 illustrates the relationship between the mantle length and the maximum length and width of the *Illex coindetii* statolith.

DISCUSSION

This paper gives a description of different developmental stages of *Illex coindetii* statoliths, based on observations of the statolith growth. There are important changes in shape of the statolith

Figure 3. Stages of development for the statolith of *Illex coindetii.* A: Stage I, maximum statolith length (MSL)= 0.67 mm and maximum statolith width (MSW)= 0.40 mm; B: Stage II, MSL =0.90 mm and MSW= 0.63 mm; C: Stage III, MSL= 1.13 mm and MSW= 0.80 mm; D: Stage IV, MSL= 1.20 mm and MSW= 0.80 mm; E: Stage V, MSL= 1.53 mm and MSW= 1.03 mm.
Figura 3. Estadíos de desarrollo del estatolito de Illex coindetii. *A: Estadío I, longitud máxima del estatolito (LME)= 0,67 mm y anchura máxima del estatolito (AME)= 0,40 mm; B: Estadío II, LME= 0,90 mm y AME= 0,63 mm; C: Estadío III, LME 1,13 mm y AME= 0,80 mm; D: Estadío IV, LME= 1,20 mm y AME= 0,80 mm; E: Estadío V, LME= 1,53 mm y AME= 1,03 mm.*

through the life cycle of *Illex coindetii.* Considering the statolith of ommastrephids, it is important to note the difficulty in differentiating between the dorsal dome and the superior and inferior lobes described by CLARKE (1978) for teuthoids. This observation agrees with SÁNCHEZ (1981) for *Illex coindetii* specimens from Mediterranean waters and ARKHIPKIN (1990) and BRUNETTI AND IVANOVIC (1991) for *Illex argentinus.* It was also observed that the rostral angle for statoliths of *Illex coindetii* juveniles is clearly higher than 140° and progressively it is getting narrower until it reaches 90° in mature animals.

Stages I and II correspond to specimens ranging from three to five months of age. The description coincides with stages I and II defined for *Illex argentinus* (BRUNETTI AND IVANOVIC, 1991) and the "definitive stage" noted by Morris and ALDRICH (1984). The shape of the statolith is enlarged to the ventral side and it grows in the ventral zone. The formation of the wing converges from two different directions, from the dorsal zone to the ventral one and vice-versa.

Stage III of the statolith of *Illex coindetii* corresponds to submature and mature animals between five and eight months of age ranging from 130 to 200

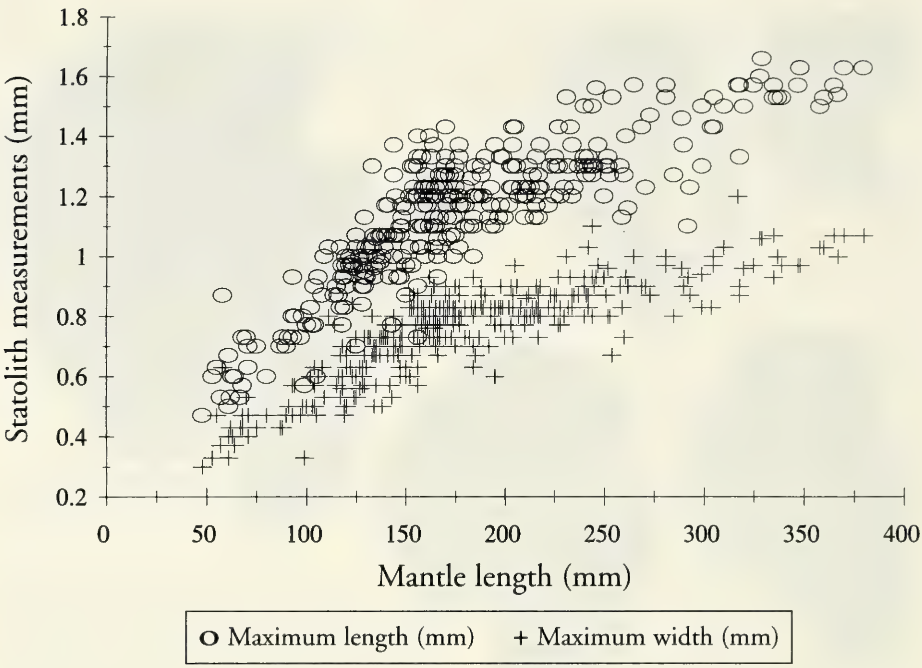

Figure 4. *Illex coindetii.* Relationship between mantle length and maximum length and width .
Figura 4. Illex coindetii. *Relación entre la longitud del manto y la anchura y longitud máximas.*

mm ML. The union of the wing with the dorsal dome of the statolith was observed in this stage, which agrees with the observations of MORRIS AND ALDRICH (1984) for the "juvenile stage" of *Illex illecebrosus* and stage III of ARKHIPKIN (1990) and BRUNETTI AND IVANOVIC (1991) for *Illex argentinus*. From this stage onwards, the growth of the statolith slows down; this could be related with the process of maturation of the animals as showed in the Figure 4. In stage III appears for the first time the foramen, which was noted as a characteristic feature of ommastrephids. This is a lack of crystallisation that runs parallel to the rostrum. It is formed when both planes of the wing grow, connecting over the medial part of the statolith, leaving one distinct zone between this point and the body of the statolith.

Stages IV and V are very similar in shape. However, a main difference can be found when the foramen disappears completely in stage V. Stage IV of *Illex coindetii* corresponded to animals of between 200 and 250 mm ML and ages ranging from eight to ten months. Finally, the statoliths of animals bigger than 250 mm ML and older than ten months are included in the stage V. These statoliths are similar to those described by MORRIS AND ALDRICH (1984) for the "advanced stage" in statoliths of *Illex illecebrosus*, to the stage VI observed by BRUNETTI AND IVANOVIC (1991) for *Illex argentinus* and the statolith described by SÁNCHEZ (1981) for an adult *Illex coindetii* specimen from the Mediterranean Sea.

On the whole, it can be concluded that the shape of the statolith changes gradually from the juvenile stage until it reaches a definitive stage of development. There are three features to be noticed during the growth of the *Illex coindetii* statolith: a) the variation of the rostral angle, getting narrow progressively, from an

angle wider than 120° in statoliths of juveniles to a 90° angle in mature animals; b) the growth of the statolith slows down when the animals reach sexual maturity; c) the rounded shape of the statolith, which makes difficult the differentiation between the dorsal dome and the lateral lobes; for this reason it is proposed to extend the term dorsal dome to the superior lobe. Therefore, the inferior lobe of the lateral dome should be called simply lateral dome.

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Doris nigricans Otto, 1823, *Nov. Act. Ac. Caes. Leop. Car.*, 10: 275.

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PORTADA DE *Iberus*

Iberus gualterianus (Linnaeus, 1758), una especie emblemática de la península Ibérica, que da nombre a la revista. Dibujo realizado por José Luis González Rebollar "Toza".

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PREFACE

This volume of *Iberus* comprises a miscellany of various papers and posters presented at the Twelfth International Malacological Congress held at Vigo (Spain) from 3 September to 8 September, 1996. This congress was organised by Dr. Ángel Guerra and Dr. Francisco Rocha, members of the Instituto de Investigaciones Marinas (IIM) on behalf of Unitas Malacologica and under the auspices of the Consejo Superior de Investigaciones Científicas (CSIC), the Sociedad Española de Malacología (SEM) and the Cephalopod International Advisory Council (CIAC).

Based at the Cultutal Center of the Caixavigo and the adjacent Casa das Artes do Concello de Vigo, the congress was attended by four houndred and twenty one specialists on molluscs from different research fields of fifty seven countries. The framework of the Vigo Congress was composed by five symposia, three free lectures and four workshops. These ranged over all Classes of Mollusca, the marine, freswater and land environments, evolution and fossil records, phylogeny and systematics, ecology, medical and applied malacology, the functional morphology of cephalopods, endemisms in the marine realm, and data bases. In addition to the communications most of the time was devoted to informal meetings and discussions.

The congress was sponsored by over fourteen Governamental and Official Institutions and companies. However, it would not be possible without the enthusiasm and the determination of the Local Organising Committee compossed mainly by people working in the research group of Ecofisiología de Cefalópodos (IIM), the Universities of Vigo and Santiago de Compostela and the Sociedad Española de Malacología (SEM). Their forsight, kindness and hard work made a very successful congress. We thank all of them and particularly to the director and the manager of IIM, Dr. Ricardo Pérez Martín and Mr. Luis Ansorena, respectively. Our acknowdlegment to Dr. Emilio Rolán, President of the SEM and co-editor of the book of abstracts[1], Mrs. María Teresa Fernández, the person in charge for all the secretariat affaires of the congress, and to all the organisers of the different sessions, who wisely managed the symposia, workshops and free lectures. We are very grateful to all the referees for their expert assistance reviewing these manuscripts. Delay in publication of this volume is basically our responsability, but we wish to point out correspondence with some of the authors was not easy.

In the oppening address to the Vigo Congress, Dr. Winston F. Ponder argued that malacology is not doing justice to the importance of molluscs. Molluscs are a large phylum of large bodied, well-known animals with a superb fossil record, excellent model organisms in evolution, genetics, physiology and ecology, economically important (fisheries and cultures), and as agricultural pests and carriers of disease. Analysis of several experts revealed, however, that few papers on molluscs are given at international meetings or published in mainstream journals, and instead, most appear in malacological meetings and journals, and much of it is narrowly focussed and trivial, indicating an inward focus and conservatism. If malacology is to improve its perception by the scientific community, the basic research must be focussed on areas of greatest interest, the study of molluscs must contribute to major areas of scientific inquiry and social and economic concern. Our discipline also needs

a strong and effective voice in the traditional (books and journals) and the new (electronic) media. This, and other issues in non-molluscan specialised journals which now are in press, must be regarded as an effort of the Vigo Congress organisers to reverse the trend of margination of molluscan studies in mainstream biology.

This volume has been published under the inestimable collaboration of the associated editors of *Iberus* D. Gonzalo Rodríguez Casero and Dr. Eugenia Martínez Cueto-Felgueroso. Nine papers are included in this volume. These articles embrace very different aspects of the malacology and comprise distincts groups of molluscs that belongs to several ecosystems. Thus, we find in this book studies which run from the biogeography and demographic response of the snail populations to enviromental conditions to the study of molluscan evolution, going through inmunology and morphological researches.

Finally, we would like to thank the Spanish Ministry of Education and Science, the Education Ministry of the Galician Government, the manager of the 5th Centenary of the Universidad de Santiago de Compostela and the Chancellor of the Universidad de Vigo for their support to organise the Twelfth International Malacological Congress and specially the Council of Unitas Malacologica for providing funds for publication of this volume of *Iberus.*

Angel Guerra and Francisco Rocha

[1] Guerra, A., E. Rolán and F. Rocha (eds.), 1995. Abstracts of the Twelfth International Malacological Congress. Vigo, 3th-8th September, 1995. Unitas Malacologica and Instituto de Investigaciones Marinas (CSIC), Vigo, Spain. 530 pp.

Phagocytosis by haemocytes from the Lesser Octopus *Eledone cirrhosa*

Fagocitosis en hemocitos del pulpo blanco *Eledone cirrhosa*

Shelagh K. MALHAM*, Norman W. RUNHAM* and Christopher J. SECOMBES**

Recibido el 8-I-1996. Aceptado el 11-IV-1996

ABSTRACT

Haemocytes from *Eledone cirrhosa* phagocytose formalized bacteria (*Vibrio anguillarum*). The phagocytic capabilities of *E. cirrhosa* haemocytes are affected by several factors, including the haemocyte culture medium, temperature, duration of the assay, and the bacterial pre-incubation conditions such as haemolymph concentration, temperature and the duration of pre-incubation.

Haemocytes will phagocytose in the absence of haemolymph. With a 30min incubation period the number of phagocytosing haemocytes increases as the pre-opsonization concentration and incubation temperature increase. However after 2 hours at 15 or 20°C the number of haemocytes phagocytosing unopsonized bacteria is equivalent to the number engulfing 100% haemolymph opsonized bacteria.

RESUMEN

Los hemocitos de *Eledone cirrhosa* fagocitan bacterias formalizadas (*Vibrio anguillarum*). La capacidad de fagocitar en estas células se ve afectada por varios factores, incluyendo el medio de cultivo de los hemocitos, temperatura, duración del experimento, y las condiciones de preincubación de las bacterias, tales como concentración de hemolinfa y temperatura y duración de la preincubación. Los hemocitos fagocitan en ausencia de hemolinfa. Con un periodo de incubación de 30 minutos, el numero de hemocitos que fagocitan se incrementa cuando lo hacen la concentración de preopsonización y la temperatura de incubación. Sin embargo, tras dos horas a 15 ó 20°C, el número de hemocitos que fagocitan bacterias no opsonizadas es equivalente al de hemocitos que fagocitan bacterias tratadas con hemolinfa al 100%.

KEY WORDS: *Eledone cirrhosa*, haemocytes, phagocytosis, opsonization.
PALABRAS CLAVE: *Eledone cirrhosa*, hemocitos, fagocitosis, opsonización.

INTRODUCTION

In vivo and *in vitro* investigations into the cellular activities of molluscs have demonstrated that, in a number of cases, the blood cells or haemocytes are avidly phagocytic and capable of recognising non-self (reviewed by MILLAR AND RATCLIFFE,

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1994). The process of phagocytosis involves a number of recognizable stages, which include attraction, attachment, ingestion and killing of foreign organisms, and is influenced by a number of factors (reviews by RATCLIFFE, ROWLEY, FITZGERALD AND RHODES, 1985; MILLAR AND RATCLIFFE, 1994). Variables which have been shown to affect phagocytic rates in molluscs include incubation temperature (FOLEY AND CHENG, 1975), time and pH (ABDUL-SALAM AND MICHELSON, 1980), the size of the particle presented for phagocytosis and the nature of the particles (reviewed by BAYNE, 1983). Though phagocytosis will take place in the absence of opsonizing agents (RENWRANTZ AND STAHMER, 1983; TUAN AND YOSHINO 1987; FRYER, HULL AND BAYNE, 1989), several experiments have shown that soluble humoral factors or opsonins may be instrumental in non-self recognition (PROWSE AND TAIT, 1969) and, or enhancement of phagocytosis (reviews by JENKIN, 1976; RATCLIFFE *ET AL.*, 1985).

The haemocyte culture medium has been shown to influence phagocytosis with, in the case of the Asian clam, *Corbicula fluminea,* the presence of divalent cations being necessary for both opsonin-independent and opsonin-dependent phagocytosis (TUAN AND YOSHINO, 1987). The process of opsonization also appears to be influenced by several other factors. FRYER AND BAYNE (1989), using *Biomphalaria glabrata,* showed that for this mollusc opsonization is a time-dependent process. Further, TRIPP (1992), working with *Mercenaria mercenaria* demonstrated that at low temperatures, opsonization caused enhanced phagocytic rates.

The octopus *Eledone cirrhosa* is benthic in habit, ranges in depth from sub-littoral to 770 m and encounters temperatures between 5 and 15°C (BOYLE, 1983). The animal has a closed circulatory system and if wounded prevents blood loss by local vasoconstriction of the area surrounding the wound. The blood of the octopod does not clot and further blood loss is prevented by allowing seepage of blood through the wound until blood cells eventually plug the wound (WELLS, 1978, 1983; BAYNE, 1983). If the animal loses a large amount of blood a dilution of the respiratory pigment (haemocyanin) occurs which takes up to 2 hours to be reversed (WELLS AND WELLS, 1993). There appears to be only one main type of blood cell or haemocyte in *E. cirrhosa.* The haemocyte matures in the white body, or haematopoetic organ, of the animal and is released into the closed circulatory system (COWDEN AND CURTIS, 1974, 1981). Few cephalopod defense mechanisms have been elucidated (FORD, 1992). It is known that *E. cirrhosa* haemocytes will phagocytose erythrocytes only in the presence of haemolymph *in vitro* (STUART, 1968). Also *in vivo* studies (STUART, 1968; BAYNE, 1973) using different octopods, demonstrate that it is mainly fixed phagocytes in certain organs which clear injected foreign particles, with haemocytes only removing a small fraction of them.

This paper investigates whether haemocytes from *E. cirrhosa* are capable of phagocytosing dead bacteria *in vitro* and whether temperature, time and haemolymph concentrations influence phagocytosis. Additional experiments were also performed to determine whether bacterial pre-incubation (opsonization) at different temperatures, times and haemolymph concentrations affected phagocytic rates.

MATERIALS AND METHODS

Animals: Octopuses, *Eledone cirrhosa* (Lamarck) were obtained from crab pots around the North Wales coast. The animals were brought into the aquarium at the University of Bangor and maintained in natural seawater at 10-12°C. After 48 h the animals were weighed, marked using a panjet and assigned to a particular tank. Five octopuses per tank were chosen at random for each set of experiments.

Haemolymph: Blood was withdrawn from the branchial blood vessel of each octopus as described by MALHAM, SECOM-

BES AND RUNHAM (1995). The blood was centrifuged at 4°C for 5 min at 800g to remove the haemocytes. The resulting haemolymph from a number of individuals was pooled and frozen at -20°C. Before use the haemolymph was thawed and diluted to a final concentration of 0. 1, 1 or 10% in Sterile Octopus Saline (SOS) (NaCl, 2.367 g/100 ml; Glucose, 1 g/100 ml; $CaCl_2$, 0.116 g/100 ml; KH_2PO_4, 0.0056 g/100 ml; KCl, 0.1089 g/100 ml; $MgSO_4{\cdot}H_2O$, 0.503 g/100 ml; $MgCl_2$, 0.419 g/100 ml).

Haemocytes: From each animal 1 ml blood samples were withdrawn into 10 ml of ice cold Marine Anticoagulant (NaCl, 2.63 g/100 ml; Glucose, 1.8 g/100 ml; Tri-Sodium Citrate, 0.088 g/ml; Citric Acid, 0.055 g/100 ml) containing ethylene glycol-bis(b-aminoethylether) N, N, N', N', -tetraacetic acid (EGTA) (0.029 g/100 ml). After a blood count the haemocytes were centrifuged at 800 g for 5 min at 4°C, and washed by resuspension in Octopus Ringer (NaCl, 2.433 g/100 ml; Glucose, 1.4 g/100 ml; EGTA, 0. 015 g/100 ml; KCl, 0.082 g/100 ml; KH_2PO_4, 0.004 g/100 ml) containing $CaCl_2$ (0.0142 g/100 ml), $MgCl_2$ (0.0524 g/100 ml) and $MgSO_4$ (0.0629 g/100 ml). A final haemocyte count was made before the haemocytes were washed for a second time and resuspended in SOS at 1×10^6 haemocytes/ml.

Bacteria: *Vibrio anguillarum* (MT275) were obtained from the Scottish Office, Agriculture and Fisheries Department, Marine Laboratory, Aberdeen. Formalized *V. anguillarum* were counted, washed twice by resuspension in SOS and centrifuged at 13000 g for 10 min before resuspension at 8×10^8 cells/ml in the required treatments.

Transmission electron microscope (T.E.M.) preparation: Five hundred μl of blood was withdrawn from the branchial blood vessel of the octopus and mixed directly with 500 μl of washed bacteria. After 2h incubation at 15°C the blood was centrifuged and the haemolymph removed. The pelleted haemocytes were fixed for 24 h at 4°C in 2.5% glutaraldehyde (in 0.1M sodium cacodylate buffer at pH 7.4). The haemocytes were washed in 0.1M sodium cacodylate buffer and secondarily fixed for 2 h at room temperature in 1% osmium tetroxide before staining *en bloc* with 2% uranyl acetate over night. The pellet was then dehydrated through ethanol and propylene oxide and embedded in Spurr resin. Cut sections (50 nm) were mounted on 100 mesh pioloform copper coated grids and stained with lead citrate. Sections were viewed in a GEC Corinth 500 at 60 KV.

Phagocytosis assay: Two phagocytosis experiments were performed to determine the effect of haemolymph concentration, temperature and time on haemocyte phagocytosis. Five animals were used for each experiment. The first experiment involved incubating haemocytes in 16 well tissue culture slides (Nunc) for 2 h at different temperatures, but utilizing one pre-incubation temperature and time for the bacteria. The second experiment involved haemocyte incubations of 30 min only and utilized different temperatures, times and haemolymph concentrations for bacterial pre-incubations.

For the first experiment 50 ml of the haemocyte suspension in SOS was put into each of the 16 well chambers of a tissue culture slide. Fifty microliters of either SOS or haemolymph diluted in SOS was added in duplicate, at half hour intervals, to selected wells. Bacteria were resuspended in either SOS or 100% haemolymph for 2 h at 15°C and washed twice before use. Fifty microliters of either SOS treated or haemolymph treated bacteria immediately followed the haemolymph additions, again in duplicate. Each well of the tissue culture slide therefore contained: 50 ml of haemocytes in SOS, 50 ml of either SOS or haemolymph diluted in SOS to 0.1, 1 or 10% concentration (final concentrations of 0.03, 0.33 or 3.33% respectively) and 50 ml of bacteria resuspended in SOS after treatment. The assays were run at four temperatures (5, 10, 15 and 20°C). After 2 h the tissue

culture slides were rinsed in SOS to remove unattached bacteria and the slide fixed by immersion in methanol for 3-5 min.

The second experiment involved the addition of 50 ml of haemocytes in SOS at 1 x 10^6 haemocytes/ml, followed by 50 ml of haemolymph diluted in SOS at 0, 0. 1, 1 or 10% concentrations and 50 ml of the different bacterial preparations added in duplicate to the tissue culture slides. The bacteria were washed and resuspended in haemolymph at concentrations of 0, 0.1, 1, 10 or 100%, using Phosphate Buffered Saline pH 7.0 (PBS, Gibco, without Ca^{2+} and Mg^{2+}) as the diluent. Bacteria were incubated for 1, 10, 60 or 120 min at 5, 10, 15 or 20°C, before being washed twice and used in the assay. The slides were incubated at temperatures of 5, 10, 15 or 20°C. After 30 min the tissue slides were rinsed with SOS and the experiment stopped by immersion of the slide in methanol as previously.

All slides were then stained in Giemsa (Sigma), rinsed in Gurr Buffer (BDH pH 6.8) and air dried before mounting using DPX.

Statistical analysis: Analysis was performed by random counting of 200 haemocytes in each well. The haemocytes were counted under oil using a compound binocular microscope at 800x magnification. All slides were numbered and randomly selected to reduce observer bias. The number of haemocytes which had phagocytosed bacteria was expressed as a percentage of the haemocytes counted in each of the duplicate wells. The results for each of the duplicate wells were averaged and analysis of variance (ANOVA) performed for the 2 experiments using the 5 replicates. In each case P values of < 0.05 were taken as being significant. The replicate means were calculated and Tukey's pairwise comparison was performed for each experiment using the calculated confidence interval estimation (CI estimation). The CI estimate allows 2 separate means to be statistically compared (Rice, 1988).

RESULTS

Phagocytosis of the formalized Gram negative bacterium, *V. anguillarum*, by *E. cirrhosa* haemocytes occurs both in the presence and absence of haemolymph. Collected haemocytes were incubated with bacteria for 2 h before fixation for T.E.M. Sections clearly indicate that *E. cirrhosa* haemocytes phagocytose and degrade bacteria (Fig. 1).

From Analysis of variance a number of significant conclusions were obtained. Phagocytosis by haemocytes following pre-incubation of the bacteria in 100% haemolymph was significantly greater than phagocytosis following SOS treatment ($F= 594.85$, $P<0.0001$) (Fig. 2). Highly significant values were also obtained for the effect of incubation temperature ($F= 155.09$, $P<0.0001$), and also for the duration of the assay ($F= 178.9$, $P<0.0001$). The concentrations of haemolymph used in the assay medium did not have a significant effect ($F= 0.32$, $P= 0.814$) indicating that the rate of phagocytosis was statistically equivalent in assays containing 0, 0.1, 1 or 10% haemolymph.

Cross-wise comparisons of the percentage of haemocytes phagocytosing opsonized and unopsonized bacteria, temperature and assay duration were also highly significant, ($P<0.0001$), whereas cross-wise comparisons involving haemolymph concentration in the assay medium, confirmed that the haemolymph concentrations, in SOS, did not affect phagocytic rates. Haemolymph concentration was therefore not considered in further analysis, and results at each temperature and time were pooled.

Phagocytosis of bacteria pre-incubated in SOS was affected by temperature and time (Fig. 2A). At all temperatures the number of haemocytes engulfing bacteria increased over time. At 20°C there appeared to be fewer haemocytes phagocytosing than at 15°C, however statistically there was no difference between the means at the 2 temperatures. At 10°C there was a rapid increase in the number of haemocytes phagocy-

Figure 1. Transmission electron micrograph of an *Eledone cirrhosa* haemocyte (H) having engulfed a bacterium (*Vibrio anguillarum*) (B). Scale bar 10 µm.
Figura 1. Microfotografía de un hemocito (H) de Eledone cirrhosa *tras haber tragado una bacteria (*Vibrio anguillarum*) (B). Escala 10 µm.*

tosing bacteria during the first 30 min followed by a slower rate of increase up to 2 h. At both 5 and 10°C significantly lower phagocytic rates were observed than at 15 and 20°C over the 2 h period. Fig. 2B shows the mean number of haemocytes phagocytosing bacteria, pre-incubated in 100% haemolymph, over time. The haemocyte phagocytic rate again increased over the 2 h period but there were far smaller differences between the incubation temperatures. The phagocytic rates were again lower at 5°C than at the other temperatures. The maximum increase in phagocytosis at all temperatures occurred within the first 30 min.

As with the first experiment, the different concentrations of haemolymph in SOS (at 0, 0.1, 1 or 10%) used in the second assay were found to have little effect, so were removed from the pair wise comparison with no appreciable percentage error increase (0.027%) and the results pooled at each pre-incubation temperature and time. To simplify the pair-wise comparison the assay temperature was not included as a main factor, but was added as an interacting factor. The results from the simplified model show that there were large statistically significant differences ($F= 1083.35$, $P<0.0001$) between the haemolymph pre-incubation concentrations. The pre-incubation temperatures ($F= 61.32$, $P<0.0001$), and the pre-incubation times ($F= 725.24$, $P<0.0001$) were similarly significantly different. Pre-incubation of the bacteria in PBS alone at different temperatures and time periods caused no significant difference in the phagocytic rate (Fig. 3). Bacteria pre-incubated in 0.1% haemolymph in PBS at all pre-incubation temperatures and times were phagocytosed at a significantly lower rate than in PBS alone. Pre-incubation of the bacteria

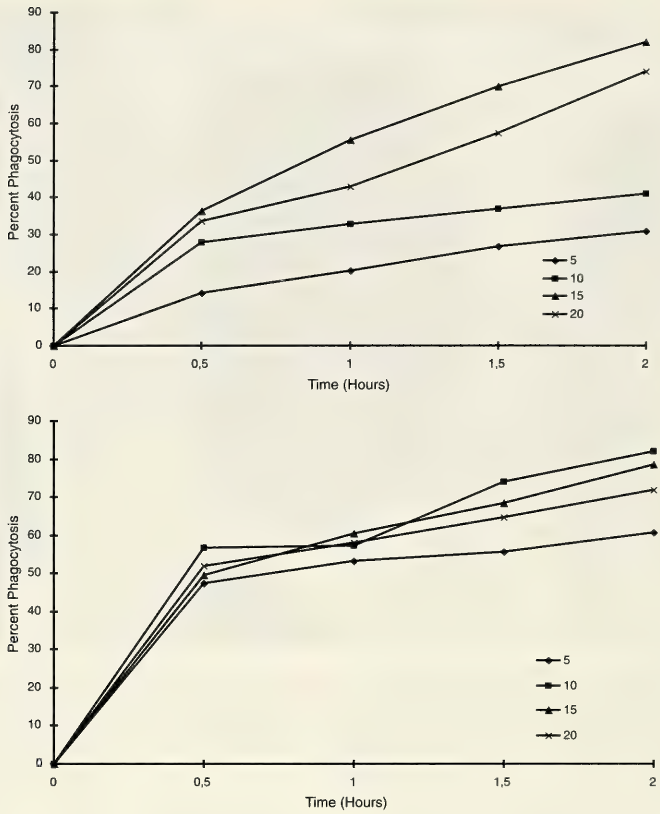

Figure 2. A: phagocytosis of non-opsonized formalized *Vibrio anguillarum* at 4 temperatures over a 2h haemocyte incubation period. The bacteria were pre-treated with SOS for 2h at 15°C. Tukeys CI estimate= 9.52. B: phagocytosis of opsonized formalized *Vibrio anguillarum* at 4 temperatures over a 2h haemocyte incubation period. The bacteria were pre-treated with 100% haemolymph for 2 h at 15°C. Tukeys CI estimate = 9.52.

Figura 2. A: fagocitosis de bacterias formalizadas Vibrio anguillarum *no opsonizadas a cuantro temperaturas sobre un periodo de incubación de hemocitos de dos horas. Las bacterias fueron pretratadas con SOS durante 2 horas a 15°C. Estimación CI de Tukeys= 9,52. B: fagocitosis de* Vibrio anguillarum *formalizado y opsonizado a cuatro temperaturas sobre un periodo de incubación de hemocitos de 2 horas. Las bacterias fueron pretratadas con hemolinfa al 100% durante 2 horas a 15°C. Estimación del intervalo de confianza de Tukeys= 9,52.*

in 1% haemolymph showed initially the same lowered phagocytic rate as for 0.1% pre-incubation. However, pre-incubation of the bacteria in 1% haemolymph for 10 min at 20°C caused an enhanced phagocytic rate which also occurred at all temperatures at 60 and 120 min. Bacteria pre-incubated in 10% haemolymph for 1 min at 5, 10, 15 and 20°C and for 10 min at 5 and 10°C were statistically equivalent to the values determined in PBS alone. However, at 10 min following pre-incubation at 15 and 20°C more haemocytes were observed phagocytosing bacteria than at 5 or 10°C, or at 1 min at all temperatures. The enhanced phagocytic rate observed using 10% haemolymph is statistically equivalent to the enhanced rate observed at 1% concentration.

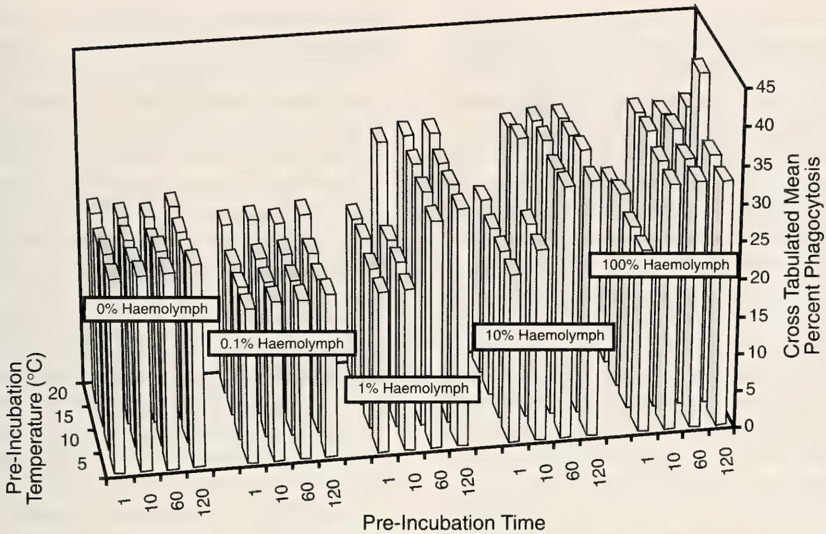

Figure 3. Phagocytosis of formalized *Vibrio anguillarum*. The haemocytes were incubated at different temperatures for 30 min only. The bacteria were pre-incubated in 0% haemolymph (*i.e.*, PBS only), 0.1% haemolymph, 1% haemolymph, 10% haemolymph and 100% haemolymph concentrations. The bacterial pre-incubation temperatures were 5, 10, 15 and 20°C and the pre-incubation times were 1, 10, 60 and 120 min. Tukeys CI estimate = 3.1.

Figura 3. Fagocitosis de Vibrio anguillarum *formalizado. Los hemocitos fueron incubados a diferentes temperaturas durante sólo 30 minutos. Las bacterias fueron preincubadas en concentraciones de hemolinfa del 0%* (i.e., *sólo PBS), 0,1%, 1%, 10% y 100%. Las temperaturas de preincubación de las bacterias fueron 5, 10, 15 y 20°C y los tiempos de preincubación de 1, 10, 60 y 120 minutos. Estimación del intervalo de confianza de Tukeys= 3,1.*

DISCUSSION

The results presented here demonstrate that *E. cirrhosa* haemocytes are capable of recognizing and ingesting the formalized bacterium *Vibrio anguillarum*. *V. anguillarum* is a Gram negative commensal marine opportunist and was chosen as the experimental bacterium because it has been isolated from, and used in previous studies on wound healing in *E. cirrhosa* (BULLOCK, POLGLASE AND PHILLIPS, 1987). This bacterium has also been implicated in causing cephalopod infections when the animals are held in captivity and is a common contributory cause of death at high aquarium temperatures (LEIBOVITZ, MEYERS AND ELSTON, 1977; HANLON, FORSYTHE, COOPER, DINUZZO, FOLSE AND KELLY, 1984; FORD, ALEXANDER, COOPER AND HANLON, 1986; HANLON AND FORSYTHE, 1990).

STUART (1968) found that *E. cirrhosa* haemocytes required haemolymph for *in vitro* phagocytosis of erythrocytes. The data presented in this paper demonstrate that the presence of haemolymph is not necessary for ingestion of bacteria. However, this bacterium is smaller with far less surface area than an erythrocyte and as such maybe more easily phagocytosed. It was found by TYSON AND JENKIN (1974) that haemocytes from a crayfish (*Parachaeraps bicarinatus*) phagocytosed bacteria in the absence of haemolymph, but erythrocytes were not phagocytosed unless they were pre-treated with haemolymph (MCKAY, JENKIN AND ROWLEY, 1969). Further JENKIN (1976), suggested that the concentration of certain recognition

molecules on the crayfish haemocyte surface was not sufficient to bind erythrocytes, but was sufficient to bind bacteria, and a similar explanation could apply to *E. cirrhosa* haemocytes. Another possibility was demonstrated by BAYNE, MOORE, CAREFOOT AND THOMPSON, (1979), who showed that haemocytes from *Mytilus californianus* had a greater affinity for yeast cells than human erythrocytes, and suggested that phagocytosis of foreign particles was selective. Results from other molluscan species also demonstrate that surface antigenicity of the respective test particles has an effect on phagocytosis by haemocytes (TRIPP AND KENT, 1967; ANDERSON AND GOOD, 1976).

TRIPP (1966), using the bivalve *M. mercenaria*, concluded that haemolymph pre-treatment of erythrocytes caused increased phagocytosis. The same experiment showed however that if untreated erythrocytes were incubated with haemocytes for longer periods of time, the same levels of phagocytosis were achieved. With *E. cirrhosa* haemocytes at 15 and 20°C the phagocytic rate is higher at 30 min for 100% haemolymph treated bacteria compared to SOS treated bacteria, but after 2 h there was no difference in phagocytic rates between the 2 treatments. The data presented here also indicate that a higher percentage of haemocytes phagocytosed haemolymph treated bacteria at 5 and 10°C over 2 h than SOS treated bacteria. TRIPP (1992) also showed that the haemocytes of *M. mercenaria* were avidly phagocytic in the absence of haemolymph, however at low temperatures, in the presence of haemolymph there was increased phagocytosis of yeast. ABDUL-SALAM AND MICHELSON (1980), working with *Biomphalaria glabrata*, also demonstrated that temperature has an effect on haemocyte phagocytosis. A phagocytic activity peak was evident at 30°C with inhibition of phagocytosis below 15°C. Low temperature inhibition (4°C) of phagocytic rates has also been demonstrated for the haemocytes from the hard clam *M. mercenaria* with maximum rates occurring at 22 and 37°C (FOLEY AND CHENG, 1975). With SOS treated bacteria, *E. cirrhosa* haemocytes demonstrate an activity peak with about 70% of haemocytes phagocytosing after 2 h at 15 and 20°C. At 5°C only 14% of haemocytes contained bacteria, whereas if the bacteria were initially pre-incubated in haemolymph before addition to the assay the phagocytic rate at 5°C increased to around 47%.

The results presented above indicate that the amount of haemolymph present in the bacterial pre-incubation medium has a dramatic effect on the number of haemocytes subsequently engulfing these bacteria within a 30 min period. Haemolymph concentrations of 0.1 and 1% in PBS, resulted in lower numbers of haemocytes phagocytosing compared to PBS alone. This inhibition changes to enhanced phagocytosis, at all higher pre-incubation concentrations. Further comparisons demonstrate that the temperature of the pre-incubation medium and particularly the duration of incubation are also important factors. The observed trends indicate that increasing the pre-incubation temperature decreases the pre-incubation time needed for enhanced phagocytosis to occur. FRYER ET AL. (1989), working on *B. glabrata*, similarly demonstrated that phagocytosis was inhibited after short pre-incubation periods, whereas longer pre-incubation periods of 1 h resulted in enhanced levels. It was suggested by the authors that initial non-specific adsorption of a variety of plasma components (opsonins) occurred onto, in their case, the yeast surface. Longer exposure to the plasma allowed more of the opsonins to bind to the yeast surface. The results from the data presented here for the different pre-incubation haemolymph concentrations and durations of exposure seem to support this hypothesis. In addition it is possible that if the temperature is increased further more of the available plasma components would adhere onto the surface of the bacterium.

When haemocytes from *E. cirrhosa* were resuspended in SOS, as stated above, there is phagocytosis of the for-

malized bacterium *V. anguillarum*. In buffers containing either EDTA or EGTA, no phagocytosis of the same bacterium was evident (Malham, unpublished data). SOS contains Ca^{2+} and Mg^{2+} and it appears likely that the presence of these divalent ions has an effect on phagocytosis. FRYER AND ADEMA (1993) showed that manipulated haemocytes from *B. glabrata* retained some phagocytic activity, but that addition of excess Ca^{2+} and Mg^{2+} to the haemocytes before the addition of the target particles enhanced their phagocytic rates. *E. cirrhosa* haemocytes were initially drawn into an anticoagulant buffer containing EGTA and washed in Octopus Ringer, also containing EGTA, before resuspension in EGTA-free-SOS, all of which could alter haemocyte behaviour and affect phagocytosis. *Corbicula fluminea* haemocytes (TUAN *ET AL.*, 1987) also required extracellular Ca^{2+} or Mg^{2+} for both opsonin-dependent and independent phagocytosis. The authors suggest that the opsonin possibly exists as a divalent cation-macromolecular complex due to the loss of enhanced phagocytosis after dialysis against EDTA and EGTA. Further, *Mytilus edulis* haemocytes phagocytosed yeast cells with high efficiency when calcium ions were present in the suspension medium, and gave similar results when haemolymph alone was added, but almost no phagocytosis was recorded with haemocytes in buffered saline (RENWRANTZ AND STAHMER, 1983). When *V. anguillarum* was resuspended in SOS, *E. cirrhosa* haemolymph diluted in SOS, or in PBS alone, there was no change in the haemocyte phagocytic rate. However, when *V. anguillarum* was resuspended in haemolymph diluted in PBS (≥ 1% haemolymph concentration) or in haemolymph alone, enhanced phagocytosis was observed.

Haemolymph lectins have been shown to act as opsonins for haemocyte phagocytosis (e. g., RENWRANTZ, 1983; RENWRANTZ 1986; SMINIA AND VAN DER KNAPP, 1986, VASTA, 1991). Agglutination results from *Octopus maya* (FISHER AND DINUZZO, 1991) further support the role of lectins in recognition of non-self. Studies using the molluscs *Mytilus edulis* (RENWRANTZ AND STAHMER, 1983) and *Lymnaea stagnalis* (VAN DER KNAPP, 1982) have demonstrated that molecules antigenically related to haemolymph lectins have been found in the cytoplasm and on the surface of haemocytes. Lectins, in particular C-type, are found in a number of invertebrates including *Octopus vulgaris*. These lectins are Ca^{2+} dependent, and these ions are required for ligand binding of the lectin (RÖGENER, RENWRANTZ AND UHLENBRUCK, 1986). STUART (1968) suggested a possible link between an opsonic factor and haemocyanin in *E. cirrhosa*. Also a lectin identified from the haemolymph of *O. vulgaris* has been shown to be similar to a haemocyanin subunit (RÖGENER, RENWRANTZ AND UHLENBRUCK, 1985). The nature of the soluble factor causing enhanced phagocytosis in *E. cirrhosa* has not been studied, however the factor(s) must be present at a high concentration, since it is effective at a haemolymph concentration of 1% at 15 and 20°C.

In conclusion, *in vitro* phagocytosis of *Vibrio anguillarum* by haemocytes from *E. cirrhosa* is aided by a component of haemolymph and is affected by temperature, duration of the assay and preincubation of the bacterium with different haemolymph concentrations. Further studies to elucidate whether *E. cirrhosa* haemocytes are capable of phagocytosing and digesting live microorganisms *in vitro* and *in vivo* are being pursued.

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New data on the morphology and the distribution of *Bulimulus corneus* Sowerby, 1833 (Gastropoda: Pulmonata: Orthalicidae) in Nicaragua

Nuevos datos sobre la morfología y la distribución de *Bulimulus corneus* Sowerby, 1833 (Gastropoda: Pulmonata: Orthalicidae) en Nicaragua

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ABSTRACT

Aspects related to the morphology and distribution of *Bulimulus corneus* Sowerby, 1833 in Nicaragua are presented. Regarding morphology, a complete redescription of the shell and the first description of the genitalia are included. The number of records have been largelly increased; from three localities mentioned in the literature to 53. The previous figures have allowed us to draw a preliminary distribution map of the species in Nicaragua, and discuss the presence of the closely related species *Bulimulus unicolor* Sowerby, 1833 in the country.

RESUMEN

Se presentan aspectos relacionados con la morfología y la distribución de *Bulimulus corneus* Sowerby, 1833 en Nicaragua. En relación con la morfología, se presenta una redescripción de la concha y la primera descripción del aparato genital. El número de registros de la especie en el país ha sido notablemente incrementado de tres a 53 localidades. Las cifras anteriores nos han permitido confeccionar un mapa preliminar de distribución para la especie en Nicaragua, así como discutir la presencia de *Bulimulus unicolor* Sowerby, 1833, una especie muy relacionada, en el país.

KEY WORDS: *Bulimulus corneus*, Orthalicidae, morphology, distribution, Nicaragua.
PALABRAS CLAVE: *Bulimulus corneus*, Orthalicidae, morfología, distribución, Nicaragua.

INTRODUCTION

According to BREURE (1979), the genus *Bulimulus* Leach, 1814 contains 88 species, distributed over the Antilles, Central America and northern South America. MARTENS (1890-1901) gave the distribution of *Bulimulus corneus* Sowerby, 1833 as from SW Mexico to the central zone of Costa Rica, there being apparently no records outside of these limits. In Nicaragua, previous reports

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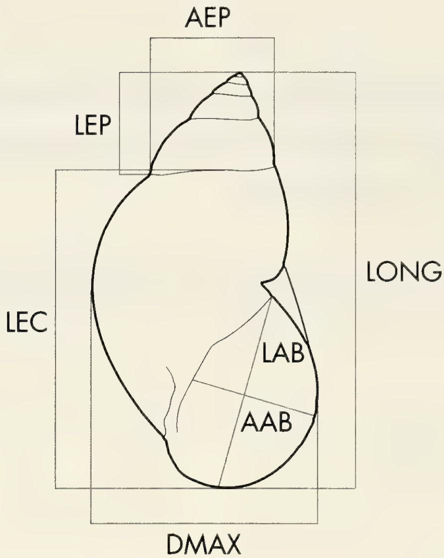

Figure 1. *Bulimulus corneus.* Shell measurements.
Abbreviations. LONG: length; DMAX: maximum diameter; LEC: height of the body whorl; DME: minimum diameter; LAB: aperture length; AAB: aperture width; LEP: spire length; AEP: spire width.
Figura 1. Bulimulus corneus. *Medidas de la concha.*
Abreviaturas. LONG: longitud; DMAX: diámetro máximo; LEC: altura de la vuelta principal; DME: diámetro mínimo; LAB: altura de la abertura; AAB: anchura de la abertura; LEP: altura de la espira; AEP: anchura de la espira.

have been from Realejo (Chinandega), San Juan Castillo (sic), El Toro rapids, RAAN (Autonomous Region of the North Atlantic) (MARTENS, 1890-1901) and Bluefields (FLUCK, 1900).

Martens stated that this species is closely related to *Bulimulus unicolor* Sowerby, 1833, and this was confirmed by PILSBRY (1897). None of the authors recognized TATE's (1870) reports of *B. unicolor* from Granada, Mesapa and San Nicolas, on the Pacific slope of Nicaragua.

The internal and external morphology of *B. corneus,* shell measurements and data on distribution were recently presented for the first time in an abstracted version (PÉREZ AND LÓPEZ, 1995), and are here given in detail. New distribution data gathered in the last few months are also presented, together with a commentary on the presence of *B. unicolor* in Nicaragua.

MATERIALS AND METHODS

All specimens were hand-collected and live specimens were relaxed in menthol and fixed in 70% alcohol. All individuals considered for the study were fully- grown adult specimens. All localities reported are additions to those previously mentioned in the literature. The list of localities is given in Table I. The distribution map was made using the UTM cartographic method with a grid size of 100 Km^2. When more than one locality occur on the same UTM 10 Km^2 quadrat, only the one that appears first in the list is mapped. The abbreviations **w. l. n.** and **Bib.** means without lot number and bibliographic locality respectively.

The variables measured in the shells are (Fig. 1): 1. length (LONG), 2. maximum diameter (DMAX), 3. height of body whorl (LEC), 4. minimum diameter (DME), 5.

aperture length (LAB), 6. aperture width (AAB), 7. spire length (LEP), 8. spire width (AEP). All measurements were made in adult specimens.

We calculated various descriptive statistics for the measured variables, in order to give a morphological description of the samples. We also used a Principal Component Analysis (PCA) to explore the variability among populations.

RESULTS AND DISCUSSION

Description: Shell (Fig. 2): Shell thin, spirally striate, corneus to brown, somewhat translucent, showing through the dark bands that stipple the mantle. Profile bulimoid-conic. Apex obtuse; protoconch typically bulimoid with sculpture of punctures in an irregular decussate pattern; whorls 5.5 to 6. Aperture ovate, margin thin, sharp, umbilicus narrow. Measurements taken on the shell are presented in Tables I and II.

Genitalia (Fig. 3): Penis with wide sheath, dilated in its central part, and reaching to more than one half of the phallus. Epiphallus approximately half as wide as penis. Flagellum thinner, approximately one half the phallus length. Sperm conduct thickened at mid-center, ending at globose spermatheca distally. Vagina more or less fusiform, slightly longer than the penis, and $^2/_3$ the width.

We have found that shell dimensions are quite variable within (Table I) and between populations (Table II), as also mentioned by PILSBRY (1897). For this reason, and because of the small total sample size (n= 44) studied from all populations (11) we have not considered the taxonomical implications of the variability. However, it should be mentioned that shell length (LONG) and height of body whorl (LEC) display the highest variances of all variables considered (Table II). Shell length is always one of the variables on which descriptions are based. We recommend caution in the use of either variables for a taxonomic characterization of the species.

It must be pointed out that THOMPSON (1967) invalidated various subspecies of the closely-related *Bulimulus unicolor* Sowerby, 1833, believing them to be variations related to climatic conditions. In this paper he considered shell length (LONG), maximum diameter (DMAX) and two other variables.

In the PCA made from conchological variables it is possible to see the marked scatter of the specimens (Fig. 4). Within the plot, there is a segregation of six individuals from the populations of El Guayabo, Granada (1), Xiloá, Managua (2), and Las Lajas, Rivas (3). It is interesting to notice that the other specimen from Rivas is located within the cloud of points. The only specimen considered from the Nicaraguan Atlantic slope (6), can be observed between the cloud of points and the six individuals previously mentioned.

Another three specimens from Ocotal (9) segregate towards the lower right corner of the scatterplot. These specimens, as the previous six, have conchological features very much like the ones from other populations (see Table I), although the ones from Ocotal have larger sizes.

In Table III, it can be seen the contribution made by each principal component to total variance. Components I (70.77%) and II (18.15%), comprise the major quantity of total variance (88.92%). The absence of negative signs (Table IV) among the eigen values obtained for component I, also with the larger contribution (70.77%), allow us to presume that it is related to size and II is related to shape. Thus, differences among populations would be apparently due to size rather than shape; and it is known that size is usually influenced by ecological factors, and consequently is highly correlated with local environmental conditions (BEROVIDES, 1988).

In their genitalia (see Figure 3), the individuals from the populations of UCA Campus (Managua Department) and Ocotal (Nueva Segovias Department) share the same external morphology and show only small differences in size of the structures. However, a more detailed anatomical analysis, including an analysis of the internal anatomy of the genital ducts (v. g. penis), of the Ocotal population is required when fresh material is available.


A
B
C

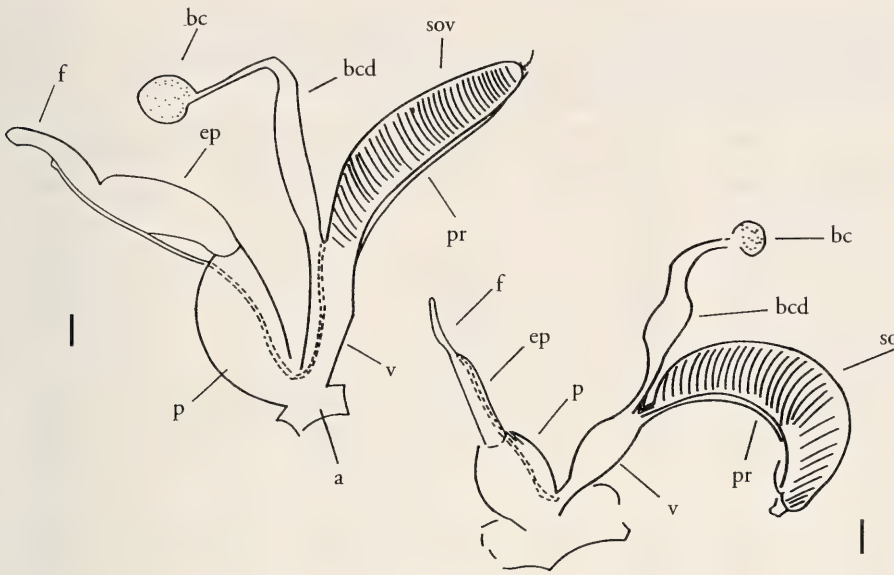

Figure 3. *Bulimulus corneus.* Genitalia. A: specimen from Ocotal; B: specimen from Campus UCA; pr: prostate; p: penis; f: flagellum; a: atrio; (sp: spermatheca)= bc: bursa copulatrix; s. ov: spermoviduct; sp. d: spermathecal duct; ep: epiphallus; v: vagina. Scale bars 1 mm.
Figura 3. Bulimulus corneus. *Aparato genital. A: ejemplar de Ocotal; B: ejemplar del Campus UCA; pr: próstata; p: pene; f: flagelo; a: atrio; (sp: espermateca)= bc: bolsa copulatriz; s. ov: espermoviducto; sp. d: conducto espermático; ep: epifalo; v: vagina. Escalas 1 mm.*

Distribution: Fifty three localities for *B. corneus* have been added to those previous recorded. They distributed over 12 Departments in the three natural regions that comprise the country (Fig. 5, Table V).

CONCLUSIONS

The distribution map gives a clear idea of *B. corneus* distribution in Nicaragua. As pointed out by JACOBSON (1968), a fairly continuos distribution can be seen among the samples, suggesting that absence in other areas is due to lack of sampling, and that *B. corneus* is widespread in the country.

B. corneus has a very wide ecological tolerance, ocurring from low altitude to more than 2000 m. The species inhabits a remarkable number of different microhabitats, including soil with herbs, soil with litter, tree trunks, logs, stones, walls of ruined houses, etc. The wide geographical distribution of the species, can pro-

(Left page). Figure 2. *Bulimulus corneus.* Shell morphology. A: Las Canoas (length 12.8 mm, diameter 7.0 mm); B: Campus UCA (length 10.6 mm, diameter 6.7 mm), C: Ocotal (length 19.9 mm, diameter 11.35 mm).
(Página izquierda). Figura 2. Bulimulus corneus. *Morfología de la concha. A: Las Canoas (longitud 12,8 mm, diámetro 7,0 mm); B: Campus UCA (longitud 10,6 mm, diámetro 6,7 mm); C: Ocotal (longitud 19,9 mm, diámetro 11,35 mm).*

Table I. Variables measured considering each sample separately (X= average, S= standard deviation). Abbreviations as in Figure 1.

Tabla I. Variables medidas considerando los ejemplares de cada muestra independientemente (X= media, S= desviación standard). Abreviaturas como en la Figura 1.

Localities	**Variables**							
	LONG	**DMAX**	**LEC**	**DME**	**LAB**	**AAB**	**LEP**	**AEP**
Xiloá (n= 6)								
X	10.93	6.70	7.14	6.13	5.51	3.87	4.38	4.85
Mín	10.10	5.80	5.5	5.30	5.1	2.95	2.9	4.5
Máx	11.70	7.50	8.6	6.5	6.0	4.7	5.8	5.4
S	0.62	0.61	1.37	0.46	0.33	0.63	1.29	0.35
Apoyo (n= 10)								
X	11.62	8.19	8.82	6.31	5.27	3.25	3.6	4.49
Mín	10.0	6.3	7.8	5.5	4.6	2.4	2.4	3.7
Máx	13.5	8.0	10.0	7.3	6.0	3.9	4.75	5.15
S	1.04	0.52	0.76	0.48	0.42	0.42	0.64	0.45
Asososca (n= 4)								
X	12.7	7.7	9.27	7.0	5.5	3.6	3.82	4.9
Mín	12.0	6.5	8.4	5.7	4.5	2.7	3.35	4.3
Máx	13.1	7.8	9.6	7.1	5.7	3.8	4.1	5.0
S	0.59	0.17	0.42	0.1	0.35	0.21	0.41	0.16
Las Canoas (n= 5)								
X	13.02	7.38	9.46	6.6	5.5	3.62	4.33	4.97
Mín	12.5	6.8	9.0	6.3	5.2	3.2	4.2	4.7
Máx	13.8	7.7	10.0	7.2	5.8	4.3	4.6	5.25
S	0.52	0.57	0.42	0.35	0.22	0.42	0.17	0.26
El Guayabo (n= 5)								
X	10.65	6.15	5.75	5.95	5.55	4.85	5.3	5.05
Mín	10.1	6.0	5.5	5.8	5.1	4.8	4.6	4.7
Máx	11.2	6.3	6.0	6.1	6.0	4.9	6.0	5.4
S	0.78	0.2	0.35	0.22	0.64	0.22	0.99	0.5
Las Lajas (n= 2)								
X	14.25	7.3	6.82	6.7	6.35	4.15	5.37	5.8
Mín	12.9	6.5	6.3	6.0	5.7	3.8	5.25	5.5
Máx	15.6	8.1	7.35	7.4	7.0	4.5	5.5	6.1
S	1.91	1.13	0.74	0.99	0.92	0.5	0.18	0.65
Tepeyac (n= 2)								
X	11.25	7.1	8.75	5.85	4.8	3.55	3.35	4.5
Mín	11.0	6.7	8.6	5.0	4.7	3.2	3.3	4.4
Máx	11.5	7.3	8.9	6.7	4.9	3.9	3.4	4.6
S	0.35	0.42	0.21	1.2	0.14	0.5	0	0.14
Ocotal (n= 4)								
X	17.12	9.52	12.57	8.72	7.9	4.92	5.40	6.16
Mín	13.6	8.0	10.5	8.0	7.4	4.2	3.8	5.25
Máx	19.9	11.35	14.2	10.0	8.4	5.2	6.9	7.2
S	2.70	2.70	1.54	0.87	0.48	0.5	1.34	0.80
Campus UCA (n= 3)								
X	11.56	7.2	8.78	6.5	5.03	3.46	3.32	4.47
Mín	10.6	6.7	8.3	6.0	4.9	3.0	2.8	4.1
Máx	12.8	7.8	9.55	7.2	5.1	3.8	3.8	4.9
S	1.12	0.55	0.63	0.64	0.12	0.42	0.50	0.41
Laurel Galán (n= 3)								
X	12.45	7.6	8.95	6.7	6.02	3.47	3.7	4.6
Mín	11.4	7.0	8.35	6.0	4.9	3.0	2.8	4.1
Máx	13.35	8.1	9.5	7.3	6.35	3.6	4.0	5.0
S	0.98	0.55	0.57	0.65	0.45	0.12	0.29	0.46

Table II. Variables measured considering all samples pooled. (X= average; Min: minimum value; Max: maximum value; S= standard deviation). Abbreviations as in Figure 1.
Tabla II. Variables medidas considerando los ejemplares de todas las muestras agrupadas. (X= media; Min: valor mínimo; Max: valor máximo; S= desviación standard). Abreviaturas como en la Figura 1.

Variables	X	Min	Max	S
LONG	12.40	10	19.90	2.02
DMAX	7.32	5.8	11.35	0.99
LEC	8.78	4.1	14.20	1.89
DME	6.59	5.0	10.00	0.89
LAB	5.64	4.5	8.40	0.87
AAB	3.70	2.4	5.30	0.67
LEP	4.12	2.4	6.90	0.97
AEP	4.86	3.7	7.20	0.64

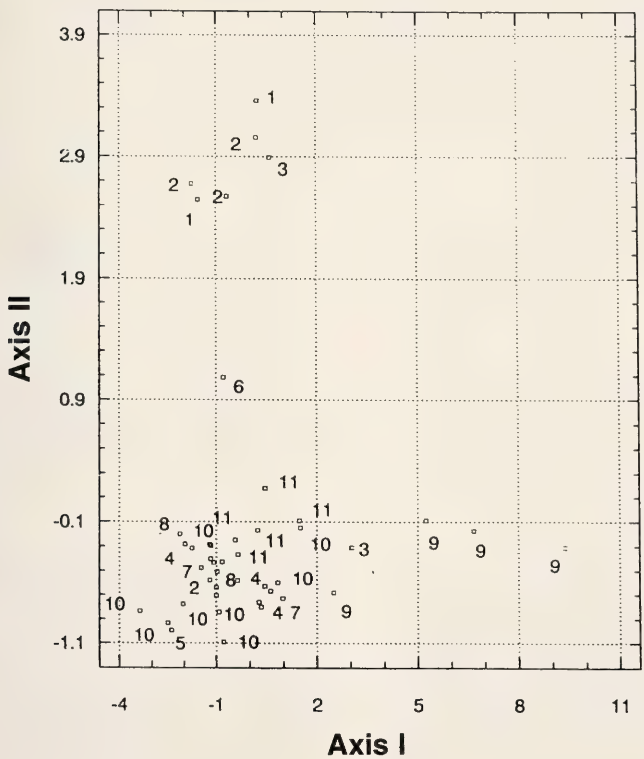

Figure 4. Axis I and II of the Principal Component Analysis. Each number represents a sample. 1: El Guayabo; 2: Xiloá; 3: Las Lajas; 4: Asososca; 5: Campus UCA; 6: Loma del Mico; 7: Laurel galán; 8: Tepeyac; 9: Ocotal; 10: Apoyo; 11: La Ceiba.
Figura 4. Ejes I y II del Análisis de Componentes Principales. Los números corresponden a las muestras. 1: El Guayabo; 2: Xiloá; 3: Las Lajas; 4: Asososca; 5: Campus UCA; 6: Loma del Mico; 7: Laurel galán; 8: Tepeyac; 9: Ocotal; 10: Apoyo; 11: La Ceiba.

Table III. Percentage of variance explained by each one of the principal components. Abbreviations as in Figure 1.
Tabla III. Porcentaje de varianza explicado por cada uno de los componentes principales. Abreviaturas como en la Figura 1.

Component	Percent of cumulative number	Variance percentage
LONG	70.77	70.77
DMAX	18.15	88.92
LEC	4.72	93.64
DME	2.23	95.88
LAB	2.06	97.95
AAB	0.89	98.84
LEP	0.71	99.55
AEP	0.44	100.00

Table IV. Eigen values obtained with Principal Component Analysis, considering axes I, II and III. Abbreviarions as in Figure 1.
Tabla IV. Valores propios obtenidos con el Análisis de Componentes Principales, considerando los ejes I, II y III. Abreviaturas como en la Figura 1.

Variables	Components		
	I	II	III
LONG	0.3995	-0.1351	0.2987
DMAX	0.3726	-0.3116	-0.0867
LEC	0.3072	-0.4996	0.0703
DME	0.3872	-0.2181	-0.2486
LAB	0.3902	0.0308	-0.0825
AAB	0.2860	0.4631	-0.7271
LEP	0.2861	0.5339	0.4999
AEP	0.3756	0.2948	0.2258

bably be explained by the numerous microhabitats that it is capable of filling.

Considering at the same time the morphological variability and the ecological range of this species, WOLDA's (1970) stament comes to mind, that variation should be understood in terms of the possibilities of survival in natural populations, and not only as a biologically isolated fact about the ecology of species.

Regarding the presence of *B. unicolor* in Nicaragua, Tate's reports were not recognized by MARTENS (1890-1901), or by PILSBRY (1897), and may have had their origin in the marked variability of *B. corneus*. We think that only *B. corneus* is found in Nicaragua.

PILSBRY (1897), mentioned Greytown (RAAN: Autonomous Region of the North Atlantic), and later Fluck (1900) gave Bluefields (RAAS: Autonomous Region of the South Atlantic) as localities for *B. unicolor* in Nicaragua. More recently, BREURE (1979) quoted Perico Island in the Bay of Panamá as the only locality in Central America.

In the last two years we have collected specimens from Bluefields, one of

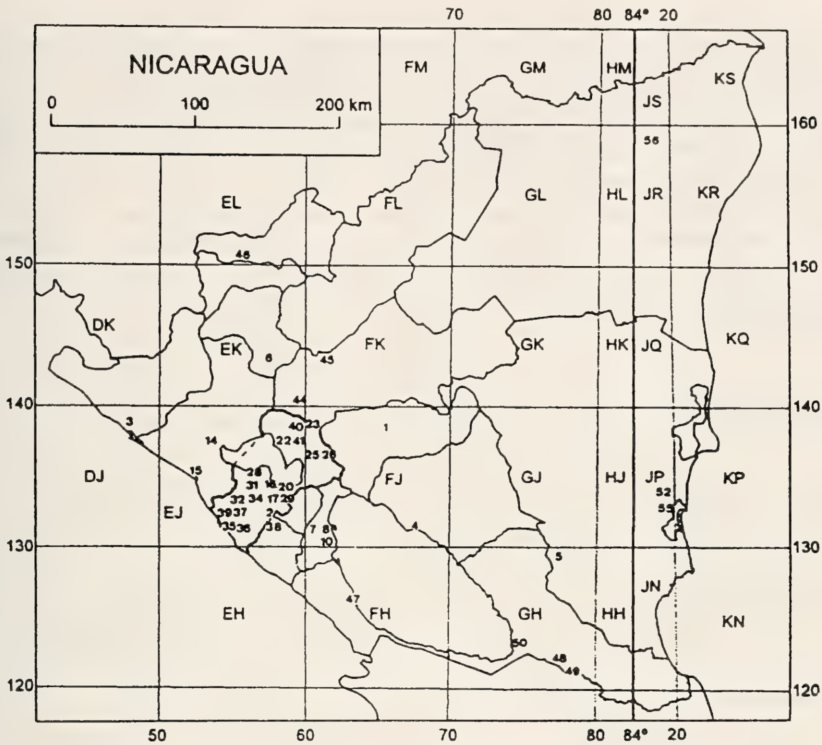

Figure 5. *Bulimulus corneus.* Distribution in Nicaragua, in UTM notation of 100 Km^2.
Figura 5. Bulimulus corneus. *Distribucion en Nicaragua, en notación UTM de 100 Km^2.*

the localities for *B. unicolor,* and two other nearby localities (Las Delicias and La Fonseca) (see Table IV). This material agrees well with the description of *B. corneus.*

We are therefore led to think either that in these localities both species live sympatrically, and we have not so far collected *B. unicolor,* or that *B. unicolor* does not occur there at all.

In view of the fact that in the revision of the subfamily BREURE (1979) did not include distribution data for *B. unicolor* in Nicaragua, and taking into account the morphological variability that THOMPSON (1967) has shown in both *B. unicolor,* and *B. corneus,* as mentioned by Pilsbry and also studied by us, we have decided for the moment to accept that the latter species is the only one that occurs in Nicaragua.

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Table V. List of new localities for *B. corneus* Sw., in Nicaragua. S= number of shells, Sa= specimens in alcohol. The samples used for statistical purposes are marked with an asterisk. Bibliographic localities are considered as Bib under "Lot number". w. l. n. means: "without lot number".
Tabla V. Lista de nuevas localidades para B. corneus Sw., en Nicaragua. S= número de conchas, Sa= especímenes en alcohol. Las muestras usadas con propósitos estadísticos aparecen marcadas con con un asterisco. Las localidades bibliográficas aparecen con la abreviatura Bib en "Lot number"; w. l. n. significa: "sin número de lote".

Code	Lot number	Localities	Coordinates Geographical	UTM	Material examined
BOACO Department					
1	92:19	El Sácal	12°33'10" N, 85°33'30" W	16PFJ 58	6S
CARAZO Department					
2	90:18	La Baronesa	12°10' N, 87°17' W	16PFJ 72	12S
CHINANDEGA Department					
3	Bib	Realejo	12°39'27" N, 83°9'18" W	16PDJ 78	?
CHONTALES Department					
4	92:14	Punta Mayal	11°52'20" N, 85°26' W	16PFJ 71	2S
5	88:30	Nueva Guinea	11°43' N, 84°57' W	16PGH 79	2S
ESTELI Department					
6	93:09	Estanzuela	13°14'04" N, 86°22'16" W	16PEK 73	2S
GRANADA Department					
7	91:26	Tepeyac	11°52.5' N, 85°59.5' W	16PFJ 01	2S(*)
8	92:01	Aguas Calientes,Cocibolca	11°52' N, 85°55'40" W	16PFJ 11	2S
9	w.l.n	Isleta de Ken	11°51'41" N, 85°53'40" W	16PFJ 11	2S
10	92:12	Laguna Blanca	11°46'15 N, 85°57'45" W	16PFJ 10	4S
11	95:72	El Guayabo	11°58' N, 85°59' W	16PFJ 11	5S(*)
12	93:10	Apoyo	11°55' N, 85°57'45" W	16PFJ 01	10S+5Sa
LEON Department					
13	90:05	Asososca	12°26' N, 86°40' W	16PEJ 37	4S(*)
14	90:06	Laguna Monte, Galán	12°26' N, 86°40' W	16PEJ 47	15S
15	88:26	Salinas Grandes	12°16'12" N, 86°30'4" W	16PEJ 25	6S
MANAGUA Department					
16	88:21	Villa Carmen	12°19' N, 86°16' W	16PEJ 74	10S+4Sa
17	88:28	Las Sierritas	12°3' N, 86°16' W	16PEJ 73	6S
18	90:07	Xiloá	12°14' N, 86°46' W	16PEJ 74	6S(*)
19	91:31	Asososca	12°18'11" N, 85°19'8" W	16PEJ 74	1S
20	92:20	Las Mercedes, Lago Xolotlán	12°9'30" N, 86°10' W	16PEJ 84	2S
21	93:39	Apoyeque	12°15' N, 86°21' W	16PEJ 74	9S
22	94:47	San Francisco Libre	12°30'12" N, 86°17'40" W	16PEJ 78	1S
23	95:01	Los Placeres, Km 63	12°33' N, 86°3'41" W	16PFJ 08	5Sa
24	95:04	Km 66.8 Carr. Matagalpa	12°29'06" N, 86°04'17" W	16PFJ 08	1Sa

Table V. Continuation.
Tabla V. Continuación.

Code	Lot number	Localities	Coordinates Geographical	UTM	Material examined
25	95:06	Km 42.5 Carr. Matagalpa	12°21′02″ N, 86°02′58″ W	16PFJ 06	7S
26	95:07	Las Canoas	12°19′00″ N, 80°00′07″ W	16PFJ 16	1S
27	95:12	Las Canoas	12°19′05″ N, 85°59′22″ W	16PFJ 06	15S
28	95:26	Mateare	12°14′10″ N, 86°25′48″ W	16PEJ 65	10S
29	95:13	Carr.Tipitapa-Masaya, Km 43	12°09′48″ N, 86°00′07″ W	16PEJ 65	10S
30	95:27	La Polvosa	12°13′24″ N, 86°24′59″ W	16PEJ 65	11S
31	95:28	Sierra de San Andrés	12°10′28″ N, 86°24′35″ W	16PEJ 64	32S
32	95:31	Nandayosi	12°06′43″ N, 86°31′14″ W	16PEJ 53	3S
33	95:32	Nandayosi, cerca del rio	12°06′54″ N, 86°30′16″ W	16PEJ 53	13S
34	95:34	Los Filos de Guajachillo	12°08′33″ N, 86°24′33 W	16PEJ 42	4S
35	95:38	San Bartolo	11°54′58′ N, 86°33′05″ W	16PEJ 41	7S
36	95:39	El Conchital	11°54′18″ N, 86°33′43″ W	16PEJ 41	15S
37	95:40	Hacienda "El Apante"	11°57′48″ N, 86°29′15″ W	16PEJ 52	3S
38	95:44	Hacienda "El Callao"	12°01′42″ N, 86°20′07″ W	16PEJ 72	14S
39	95:45	Samaria	11°59′13″ N, 86°32′39″ W	16PEJ 42	2S
40	95:57	El Tamarindo	12°29′37″ N, 86°05′01″ W	16PEJ 98	3S
41	95:59	El Platanal	12°27′06″ N, 86°05′02″ W	16PEJ 97	1S
42	95:64	Carr.Sur, Km 15.5, INCAE	10°03′13″ N, 86°18′33″ W	16PEJ 73	1S
43	95:72	Campus UCA	12°07′30″ N, 86°16′13″ W	16PEJ 74	3Sa(*)
MATAGALPA Department					
44	92:83	Ciudad Darío	12°43′50″ N, 86°11′53″ W	16PEK 90	13S
45	92:88	Fuentepura	12°58′ N, 86°55′ W	16PFK 13	2S
NUEVA SEGOVIAS Department					
46	94:59	Ocotal	13°36′35″ N, 86°28′18″ W	16PEL 51	5S(*)
RIVAS Department					
47	92:39	Río Las Lajas	11° N, 85° W	16PFH 35	2S(*)
RIO SAN JUAN Department					
48	92:24	La Toboba	11°8′ N, 84°57′50″ W	16PGH 72	2S
49	92:25	El Castillo	11°7′20″ N, 84°24′ W	16PGH 81	5S
50	w.l.n	San Carlos	12°7′20″ N, 86°46′ W	16PGH 43	7S
51	92:26	Laurel Galán	12°7′ N, 86°46′ W	16PGH 43	3S(*)
RAAS (AUTONOMOUS REGION OF THE SOUTH ATLANTIC)					
52	93:23C	Las Delicias	12°16′12″ N, 83°52′50″ W	17PJP	5S
53	93:23B	La Fonseca	12°15′36″ N, 83°58′48″ W	17PJP	2S
54	94:19	Loma del Mico	12°4′24″ N, 83°47′42″ W	17PJP	1S(*)
55	Bib	Bluefields	12° N, 83°44′18″ W	17PJP	?
RAAN (AUTONOMOUS REGION OF THE NORTH ATLANTIC)					
56	Bib	San Juan Castillo	14°24′ N, 83°54′54″ W	17PJR	?

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Phenological patterns and life history tactics of Helicoidea (Gastropoda, Pulmonata) snails from Northern Greece

Patrones fenológicos y estrategias de vida en Helicoidea (Gastropoda, Pulmonata) del Norte de Grecia

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ABSTRACT

The present study mainly concerns with the differences in the biological cycles and strategies adopted by different Helicoidea snail species. In Northern Greece the climatic conditions are not very uniform. Some snails breed during the same period as in Northern Europe but most breed in autumn, as species from Southern Europe do. Breeding may take place in all seasons except in winter, and seems to be species-specific. Long-lived snails of big size differ from short-lived species of small size as to the time of their breeding period. The climatic conditions affect the time of the breeding season and their whole life cycle and phenologies. Environmental variables in Northern Greece are strongly seasonal and thus Helicoidea snails exhibit predictable oscillations in their activity patterns, which can be interpreted by the demographic response of the populations. Terrestrial snails seem to follow two different phenologic curve types: the semelparous and short-lived species populations show a more stable phenological pattern than the biennial and pluriennial ones, who mature after the first year of their lives, being more plastic trying to face the climatic differences from one year to another.

RESUMEN

El presente estudio trata de las diferencias en los ciclos biológicos y a las estrategias adoptadas por diferentes especies de Helicoidea. En el norte de Grecia, las condiciones climáticas no son muy uniformes. Algunas especies crían durante el mismo periodo en que lo hacen en el N de Europa, pero la mayoría lo hacen en otoño, como sucede en especies del S del continente. La cría puede tener lugar durante casi todas las estaciones, excepto el invierno, y el periodo parece ser específico para cada especie. Las especies longevas y de gran talla difieren de las de pequeño tamaño y vida más corta en la duración de su ciclo de cría. Las condiciones climáticas afectan al momento de la temporada de cría y a todo su ciclo vital y fenología. Las variables ambientales son fuertemente estacionales, así que aparecen oscilaciones predecibles en los patrones de actividad, que pueden ser interpretadas por la respuesta demográfica de las poblaciones. Las babosas parecen seguir dos tipos de curvas fenológicas distintas. Las especies semelpáricas y de corta vida muestran un patrón fenológico más estable que el de especies bianuales y prurianuales, que maduran tras el primer año de vida y son más flexibles a la hora de enfrentarse a las diferencias climáticas interanuales.

KEY WORDS: Biological cycle, phenology, Northern Greece, Helicoidea, *Helix*, *Eobania*, *Helicella*, *Monacha*, *Bradybaena*.
PALABRAS CLAVE: ciclo biológico, fenología, N Grecia, Helicoidea, *Helix*, *Eobania*, *Helicella*, *Monacha*, *Bradybaena*.

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INTRODUCTION

Greece has a Mediterranean climate which is differentiated mainly along a northern-southern gradient. In Northern Greece climate is transient from Mediterranean (mostly coastal areas) to temperate (inland areas). A typical characteristic of this climate type is the coincidence of high temperatures and low precipitations during summer (lasting from June to October). The wet season is divided by a cold winter which is milder in the coastal areas. Drought is a strong agent controlling population dynamics and activity of most soil invertebrates as it imposes a pause in most physiological activities. Low temperatures during winter are also important for population dynamics and activity as they impose hibernation in some of the invertebrates e. g. terrestrial gastropods. So observed discontinuities in population development during the transition from the favourable to the unfavourable seasons and vice-versa may be attributed to environmental thresholds.

Although the association between climate and life history phenomena is self evident, it can vary among terrestrial molluscs, even between populations of the same species. Phenology reflects certain aspects of the demography of a population, that is the timing of its life cycle characteristics in a given environment. The classification of phenological patterns into categories or types (WOLDA, 1988) is better by using phenological models (VAN STRAALEN, 1982; STAMOU, ASIKIDIS, ARGYROPOULOU AND SGARDELIS, 1993). Using a phenological model, complex phenograms can be classified into types considering their skewness, curtosis, phase and period.

The aim of the present study was to find out whether terrestrial gastropods adopt a general phenological pattern if they are differentiated according to their origin, or their biotopes (inland and coastal areas) or life spans. The present study is a part of an extensive research done on the distribution and ecology of Helicoidea gastropods in Northern Greece (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1981, 1985, 1991; STAIKOU, LAZARIDOU-DIMITRIADOU AND FARMAKIS, 1988; HATZIIOANNOU, ELEUTHERIADIS AND LAZARIDOU-DIMITRIADOU, 1989; STAIKOU, LAZARIDOU-DIMITRIADOU AND PANA, 1990; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990, 1991).

MATERIALS AND METHODS

Data used derived from monthly quantitative samplings of Helicoidea snails from different parts of Northern Greece. The following species were studied: Family Bradybaenidae, *Bradybaena fruticum* (Müller, 1774); Family Helicidae, *Cepaea vindobonensis* (Férussac, 1821), *Eobania vermiculata* (Müller, 1774), *Helix lucorum* Linnaeus, 1758, *Helicella (Xerothracia) pappi* (Schüt, 1962), *Helix figulina* (Rossmässler, 1839), *Helix pomatia rhodopensis* Kobelt, 1906, *Theba pisana* (Müller, 1774); Family Hygromiidae, *Cernuella virgata* (Da Costa, 1778), *Monacha cartusiana* (Müller, 1774), *Xerolenta obvia* (Menke, 1828), *Xeropicta arenosa* Ziegler, 1836, *Xerotricha conspurcata* (Draparnaud, 1801). Sampling lasted two or four years depending on the species and their life span (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1981, 1985, 1991; STAIKOU *ET AL.*, 1988; STAIKOU *ET AL.*, 1990; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990, 1991). Details regarding the sites and the sampling procedures are given in previous studies on these species (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985, 1991; STAIKOU *ET AL.*, 1988). Ombrothermic data for Northern Greece from 1980 to 1990 are given in Figure 1. Data were provided by Mahairas P., Professor of Climatology from the Aristotle University of Thessaloniki.

Fischer's exact test for independence in 2 x 2 contingency tables (ZAR, 1984) was used for comparisons between the different categories, e. g. snails with autumnal and vernal-estival reproductive periods, long-lived (> 3 years) and

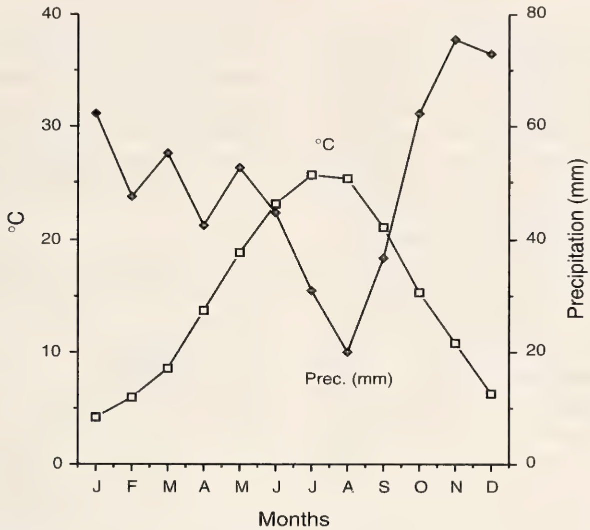

Figure 1. Ombrothermic diagram from Northern Greece. Temperature: open squares; Precipitation: solid rhombus.

Figura 1. Diagrama ombrotérmico del Norte de Grecia. Temperatura: cuadrados abiertos; Precipitación: rombos sólidos.

short-lived snail species (up to 3 years), large (largest shell diameter > 25 mm) and small sized snails.

The phenological pattern of Helicoidea species was studied by using the phenological model applied for the study of microarthropods (STAMOU *ET AL.*, 1993). In short, in this model when asymmetries and discontinuities are displayed the scales of the time-axis were adjusted. Changing time scales results in the definition of a new variable termed ecological time (ET), which is a function of a standard clock time (STAMOU *ET AL.*, 1993). This technique is based upon the following considerations: 1) the timing of a population in the field is determined by the sequence of demographic events and/or behavioural characteristics (i. e. migratory), and 2) the rate of the demographic events depends on the fluctuations of environmental variables.

In this model it is assumed that the phenology of any population inhabiting a seasonal environment can be described by a symmetric periodic curve:

$$f(\mathrm{ET}) = \mathrm{EXP}(\alpha + b \times \mathrm{COS}(2\pi \times (\mathrm{ET} - \varphi / T)) \quad (1)$$

where the independent variable ET, termed Ecological time, is a function of standard clock time (ST), ET = f (ST). In the course of standard time, ecological time is going faster during periods of sharp changes in abundance and slower during periods of abundance stability. Thus, the proposed equation describing the length of the Ecological time unit (ΔET) as a function of Standard time ST is:

$$\Delta \mathrm{ET} = f\ (\mathrm{ST}) = \mathrm{EXP}(\alpha_1 + b_1 \times \mathrm{COS}(2\pi \times (\mathrm{ST} - \varphi_1)/T_1)) \quad (2)$$

The model has eight parameters of which the period T and the phase φ of the phenogram, as well as period T_1 and the phase φ_1 of the function relating ET to ST, are the most important. The period T and the phase φ of the phenograms are expressed formally in ET units. For convenience they could be expressed in ST units (as T' and φ') by using equation (2) for the calculation of

the Standard time T′ or φ′ which corresponds to T or φ units in the Ecological time-scale (see STAMOU *ET AL.*, 1993: fig. 1). For the comparison of phenograms two more parameters can be derived: a) an estimation of the sharpness (curtosis) of the phenogram $C=(R_2-R_1)/T'$, where (R_2-R_1) is the time interval around the phase φ′, during which the abundance is above overall mean, and b) an estimation of the skewness of the phenogram $S= (\varphi'-\varphi_m)/T'$ where φ_m is the time (in ST units) when the abundance of the population is at minimum. Thus, phenograms displaying a peak at $\varphi'-\varphi_m = T'/2$ (half period) is symmetric (S= 0.5), phenograms displaying a peak soon after the minimum (S< 0.5) are positively skewed, and phenograms with S> 0.5 are negatively skewed. The model was fitted on log-transformed census data. For ET_i= f (ST_i) given as a time vector and for a given set of φ and T, the parameters a and b were estimated by least-square regression.

RESULTS

The model fitted to census data for snail populations sampled at monthly intervals from different areas are shown in Figure 2. The values of the most important parameters of the fitted phenological model are given in Table I.

In all but two examined cases the phenological pattern was strongly seasonal (Fig. 2), with a more or less 1 year periodicity apart from *Monacha cartusiana* which seems to display a six months periodicity at least during 1984 (Table I). Abundance of *Bradybaena fruticum* and *Eobania vermiculata* fluctuated almost randomly throughout the year.

Population densities of the different species do not exhibit phase synchronization. Even different populations of the same species do not always exhibit a peak density at the same time of the year. Furthermore even the same population displays a phase instability during successive years of study. For instance *Xerolenta obvia* from Paleokastro peaked either in January or in April (φ_j in Table I). *X. obvia* from Karvali peaked in July. *Helix lucorum* displayed a similar interannual instability. In both cases the shift in phase seems to be associated with an unexpected change of the weather, an extended dryness (STAIKOU *ET AL.*, 1988: fig. 2) which provoked an overall decline of the population density (Fig. 2).

The phase expressed as months after minimum population densities (φm) (Table I) is a measure of the rate of population increase from absolute minimum to peak densities. φ_m might have lower values when the time needed for a species to mature is short. Minimum φ_m values were estimated for *X. obvia* in Paleokastro, the 1st and the third year of study, indicating a rapid population growth which occurs in a period of about 3 months (Fig. 2). In Karvali, where *X. obvia* gets mature in 2 years, φ_m value was larger (Table I), as was the case with *M. cartusiana* in 1985. *Helicella (Xerothracia) pappi* snails that need 2-3 years to mature exhibited larger φ_m values, and *H. lucorum* snails which need 3-4 years exhibited the largest value of all except in 1983.

Species that mature in one year, exhibit a very rapid population growth just after the adverse period, which is winter, and consequently they are positively skewed. Species that mature in 2-3 years are negatively skewed (Table II, Fig. 3). In this case the phenological pattern may be positively skewed or symmetrical but the population remains active for longer periods and the phenological pattern is platycurtic (Table II, Fig. 3). Whereas species that mature in one year usually display a leptocurtic phenology (Table II, Fig. 3). The only species population that showed both a negatively and a positively skewed phenological pattern was *H. lucorum.*

The positively skewed phenograms are leptocurtic when they concern snail species populations that mature in one year whereas they may be slightly platycurtic when they live in regions where favourable conditions last longer as is the case of *Xeropicta arenosa* Ziegler in Edessa. Pluriennial snail species popula-

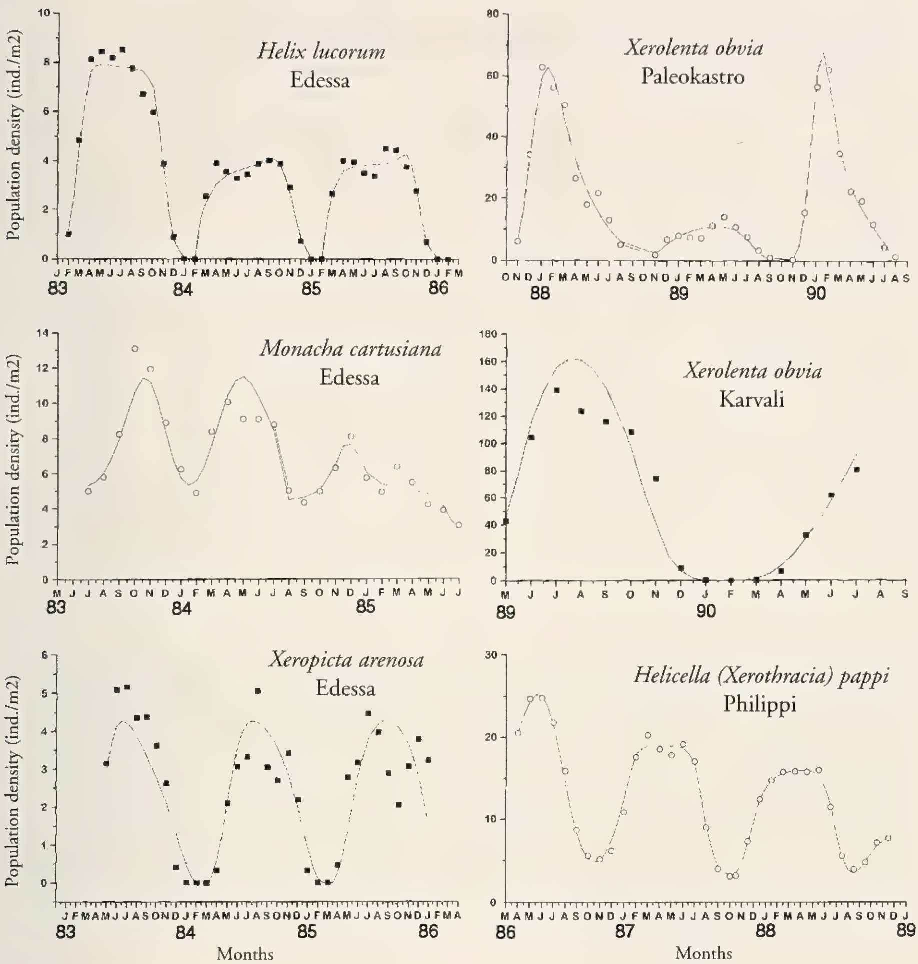

Figure 2. Abundance variations of Helicoidea snails from Northern Greece. Line: model estimates; asterisks: observations.

Figura 2. Variaciones de la abundancia de caracoles helícidos del Norte de Grecia. Línea: estimaciones del modelo; asteriscos: observaciones.

tions usually exhibit platycurtic phenological patterns, too, since their adults diapause and hide in the soil or under plants and do not emerge massively. Negatively skewed and symmetric phenograms are usually platycurtic.

It seems that there are no negatively skewed-leptocurtic species except for *M. cartusiana* that is negatively skewed and slightly leptocurtic.

Maximum activity duration is about the same for different populations of the same species or for the same population during successive years of study (Table I, MA column).

In Northern Greece long-lived species are of big size and short-lived are of small size (χ^2= 9.983, P= 0.001). Additionally, short-lived species breed in autumn whereas long-lived species may breed in autumn or vernal-estival period (χ^2= 4.261, P= 0.039) (Table III). In Northern Greece bigger helicids may breed during the vernal-estival or

Table I. The estimated parameters of the fitted model in standard time units (months).
Tabla I. Parámetros estimados del modelo ajustado en unidades de tiempo standard (meses).

Species	Place	Year	Period T (Months)	Phase φj (Months after January)	Phase φm (Months after minimum density)	Maximum activity period MA (Monthts)	R^2	Years up to matutity
Helicella pappi	Philippi	1987	12.6	2.9	5.9	7.1	0.93	2-3
		1988	10.5	3.4	6.8	6.9	0.95	
Xerolenta obvia	Karvali	1990	12.6	6.7	4.7	4.4	0.79	2
	Paleokastro	1988	14.2	0.3	2.9	4.2	0.84	1
		1989	10.8	3.5	5.7	7.3	0.77	
		1990	10.4	0.2	2.8	2.9	0.91	
Xeropicta arenosa	Potidea	1979	12.7	6.1	5.5	5.1	0.87	1
		1980	11.2	6.2	3.1	6.9	0.88	
	Edessa	1984	12.5	6.6	4.9	6.7	0.69	1
		1985	12.3	7.8	5.8	6.9	0.68	
Monacha cartusiana	Edessa	1984	6.5	-2.4	3.7	3.2	0.53	1
		1985	13.0	-1.1	6.2	4.3	0.45	2
Helix lucorum		1983	12.5	4.1	5.0	8.1	0.94	3-4
		1984	12.0	8.4	7.9	8.5	0.84	
		1985	12.0	8.9	8.5	8.2	0.86	

Table II. Skewness (negatively skewed <0.5; positively skewed >0.5) and curtosis (leptocurtic <0.5; platycurtic >0.5) from the phenograms of Helicoidea snails from Northern Greece). Abbreviations: Phil: Philippi; Pal: Paleokastro area; Kar: Karvali; Pot: Potidea; E: Edessa (the paranthesis means slightly).
Tabla II. Desviación (desviado negativamente <0,5; desviado positivamente >0,5) y curtosis (leptocúrtico <0,5; platicúrico >0,5) en los fenogramas de caracoles helícidos del Norte de Grecia. Abreviaturas: Phil: Philippi; Pal: Paleokastro area; Kar: Karvali; Pot: Potidea; E: Edessa (los paréntesis significan ligeramente).

Species	Place and Year	Positively skewed	Negatively skewed	Symmetric	Leptocurtic	Platycurtic	Mesocurtic	Years up to maturity
Helicella pappi	Phil. 1987			(+)		+		2-3
	1988		+			+		
Xerolenta obvia	Paleo. 1988	+			+			1
	1989			(+)		+		
	1990	+			+			
	Karv. 1990	+			+		(+)	2
Xeropicta arenosa	Potid. 1979				+		(+)	1
	1980	+				+		
	Edes. 1984	+				+		1
	1985	+				+		
Monacha cartusiana	Edes. 1983		+		(+)			2
	1984			+			+	1
	1985	+		(+)	+			2
Helix lucorum	Edes. 1983	+				+		3-4
	1984		+			+		
	1985		+			+		

autumnal period and small ones breed mainly in autumn (χ^2= 4.261, P= 0.039) (Table III). In coastal areas the duration of the reproductive period is very short whereas in the inland areas it is variable according to the species.

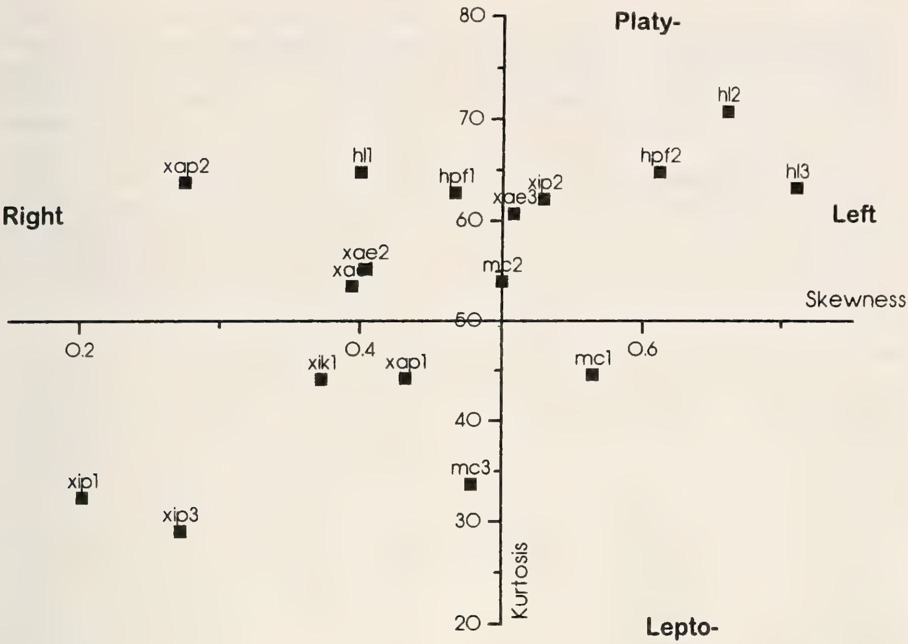

Figure 3. Ordination of phenograms into skewness(S)- curtosis (C) plane (Skewness: negatively skewed< 0.5; positively skewed> 0.5. Curtosis: leptocurtic< 0.5; platycurtic> 0.5) of Helicoidea snails from Northern Greece. Numbers denote 1st, 2d or 3d generation. Abbreviations, xap: *Xeropicta arenosa* Potidea; xae: *Xeropicta arenosa* Edessa; hl: *Helix lucorum*; hpf: *Helicella pappi* Philippi; mc: *Monacha cartusiana*; xip: *Xerolenta obvia* Paleokastro.

Figura 3. Ordenación de fenogramas respecto al plano desviación (S)- curtosis (C) (Desviación: negativa< 0,5; positiva> 0,5. Curtosis: leptocúrtico< 0,5; platicúrtico> 0,5) de babosas de la familia Helicoidea del Norte de Grecia. Los número denotan las primera, segunda y tercera generaciones. Abreviaturas, xap: Xeropicta arenosa *Potidea; xae:* Xeropicta arenosa *Edessa; hl:* Helix lucorum*; hpf:* Helicella pappi *Philippi; mc:* Monacha cartusiana*; xip:* Xerolenta obvia *Paleokastro.*

DISCUSSION

In Northern Greece the climatic conditions are not uniform (HATZIIOANNOU ET AL., 1989). The ombrothermic diagram for Northern Greece (Fig. 1) from 1980 to 1990 shows that the dry season is from June to October, whilst the wet season is divided by a cold winter period. Breeding may take place almost in all seasons except during winter. In Northern Greece, snails mainly breed from April to the end of autumn. The strong seasonality of the climate imposes a seasonal pattern of breeding. Consequently, there are two main breeding periods: the autumnal breeding period starts with the first rainfalls and stops with low temperatures (LAZARIDOU-DIMITRIADOU, 1981; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1991) and the vernal-estival breeding period which starts when the mean monthly temperature rises over 10°C and stops when the arid period starts (LAZARIDOU-DIMITRIADOU, 1981; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985; STAIKOU ET AL., 1988). Most of the land snails though, mainly short-lived and small snails, breed during the autumnal period (Table III) as Helicoidea species from Southern Europe do (CHATFIELD, 1968; REAL AND REAL-TESTUD, 1983; HELLER, 1982; SACCHI,

Table III. Life cycle characteristics from Helicoidea snails from Northern Greece. Abbreviations: D: largest shell diameter. Ehinos is found in Rhodope area, Edessa and Thessaloniki in North Central Macedonia, Philippi and Karvali near Kavala, and Paleokastro and Potidea in Chalkidiki. Abbreviations, Y: years up to maturity; SL: short lived < 3 years; LL: long lived > 3 years; SS: small sized D < 25 mm; LS: large sized D > 25 mm; V: vernal-estival reproductive period; A: automnal reproductive period.

Tabla III. Características del ciclo de vida de los caracoles helícidos del Norte de Grecia. Abreviaturas: D: mayor diámetro de la concha. Ehinos se encuentra en el área de Rhodope, Edessa y Thessaloniki al Norte de Macedonia, Phillipi y Karvali cerca de Kavala, y Paleokastro y Potidea en Chalkidiki. Abreviaturas, Y: años hasta la madurez; SL: vida corta < 3 años; LL: vida larga > 3 años; SS: pequeña talla D < 25 mm; LS: gran talla D > 25 mm; V: periodo reproductivo estival; A: periodo reproductivo otoñal.

Species	Locality	Longitude	Latitude	Y	SL	LL	SS	LS	V	A
Helix pomatia rhodopensis	Ehinos	24° 58′ 34″	41° 16′ 50″	3		+		+	+	
Helix lucorum	Edessa	22° 3′ 14′	40° 47′ 47″	3-4		+		+	+	
Monacha cartusiana				2	+		+			+
(rarely)				1	+		+		+	
Bradybaena fruticum	Edessa			2		+	+		+	
Cepaea vindobonensis	Edessa			2		+		+	+	
Helix figulina	Thessaloniki	22° 57′ 29″	41° 24′ 26″	2		+		+		+
Theba pisana	Thessaloniki			2	+		+			+
Xerotricha conspurcata	Thessaloniki			1	+		+			+
Eobania vermiculata	Thessaloniki			2		+		+		+
Helicella (Xerothracia) pappi	Philippi	24° 15′ 48″	41° 2′ 26′	2-3	+		+			+
Xerolenta obvia	Paleokastro	23° 25′ 9″	40° 24′ 59″	1	+		+			+
	Karvali	24° 30′ 11″	40° 59′ 44″	2	+		+			+
Xeropicta arenosa	Potidea	23° 19′ 24″	40° 11′ 24″	1	+		+			+
	Edessa	22° 3′ 14″	40° 47′ 47″	1	+		+			+
Cernuella virgata	Potidea	23° 19′ 24″	40° 11′ 24″	1	+		+			+

1971; BONAVITA AND BONAVITA, 1962; DEBLOCK AND HOESTLANDT, 1967) and only some breed during the vernal period as land snails from Northern Europe do (POLARD, 1975; WOLDA AND KREULEN, 1973). *M. cartusiana*, which is of Northern origin, breeds in both seasons (STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990). Estival breeding period happens in places with a wet climate during summer months (STAIKOU *ET AL.*, 1988). In areas where different species coexist (as in Logos area in Edessa) although the climatic conditions are the same the species do not breed during the same period provoking less antagonistic intraspecific reactions to their hatchings (STAIKOU *ET AL.*, 1988). Semelparous species with an r-strategy synchronize their breeding period with the favourable period which is October-mid November (LAZARIDOU-DIMITRIADOU, 1981, 1995; LAZARIDOU-DIMITRIADOU AND KATTOULAS, 1985).

There is also a marked difference between the snail species living along the sea shore and the inland ones. Coupling and laying of eggs is more or less synchronous for the populations living along the seashore and do not last more than a week each. On the contrary breeding lasts about a month for the inland species (LAZARIDOU-DIMITRIADOU, 1981; STAIKOU AND LAZARIDOU-DIMITRIADOU, 1991).

The climatic conditions under which the land molluscs live do not only affect the time of the breeding season but also their whole life cycle and phenologies. *X. obvia* needs two years to mature in coastal or semi-coastal areas and one year on the mountains (e. g. Paleokastro,

Central Chalkidiki, unpublished data). Similarly, *M. cartusiana* which is of northern origin needs two years to mature in the south instead of one, because it has to face the summer aestivation, although 15% of its population in Edessa tends to be semelparous (STAIKOU AND LAZARIDOU-DIMITRIADOU, 1990), as in Northern Europe (CHATFIELD, 1968).

Species like *B. fruticum* and *E. vermiculata* which are iteroparous and univoltine species, living for a few years, exhibit no seasonal trend of abundance but fluctuate almost randomly during the year. These show rather stable patterns despite the oscillations of environmental parameters. All the rest of the studied Helicoidea species can encounter seasonality by adjusting the timing of their vital activities. They respond to the adverse period of the year, which is winter time for Northern Greece, by displaying asymmetric (positively or negatively skewed phenograms) seasonal patterns of abundance variation. These patterns reflect a differential response of the species to tolerance against stress which seems not to be region-specific but species-specific. The annual or biennial r-strategists *(X. arenosa, X. obvia)* show a positively skewed phenological pattern due to the rapid development of juveniles soon after the adverse winter period. These juveniles have been hatched in autumn but stayed buried in the soil during winter. Their growth stops before summer dryness during which the genitalia and the gonad maturation take place and the snails are ready to lay eggs before their death in autumn. On the contrary, populations of pluriennial species are characterized by low abundance during the onset of the adverse period and a negatively skewed or symmetric phenological pattern. It seems that the growth rate of juveniles is much slower than that of annual species. The only species population that showed both a negatively and a positively skewed phenological pattern was *H. lucorum*. However, a positively skewed pattern in 1983, that is a rapid growth of population density was probable just after the adverse period since a massive emergence from hibernation of adult snails took place because of good weather conditions which started earlier than usually (STAIKOU *ET AL.*, 1988: fig. 2). Additionally, this species has a low net reproductive rate (Ro = 0.9) and a low annual turnover ratio (P/B = 1.24), the snails live up to 12 years and they mature after the third year of their lives (STAIKOU *ET AL.*, 1988).

Negatively skewed and leptocurtic phenograms could not be characteristic of a snail species since it would mean that this population would grow slowly and steadily during the favourable period of the year and would introduce rapidly growing immature snails just before the adverse period. This would be possible only if immature snails were more resistant and tolerant to the stress. Such a phenology has not also been recorded in acari or collembola (STAMOU *ET AL.*, 1993; SGARDELIS, SARKAR, ASIKIDIS, CANCELA DA FONCECA AND STAMOU, 1993). However, *M. cartusiana* is a case of negatively skewed and slightly leptocurtic phenology. In this population 15% of juveniles mature in one year as it happens in Northern Europe. So, in 1984 the dry season (summer time) was interrupted by a wet period (STAIKOU *ET AL.*, 1988: fig. 2) and this 15% of juveniles, which had already matured, managed to lay eggs before the majority of the snails which were mature and ready to copulate and lay eggs in autumn. This population, though, comes from Northern Europe and it is found in the southern limits of its distribution.

To sum up, environmental variables in Northern Greece are strongly seasonal and thus Helicoidea snails exhibit predictable oscillations in their activity patterns, which can be interpreted by the demographic response of the populations as it has been found with soil microarthropods (STAMOU *ET AL.*, 1993; SGARDELIS *ET AL.*, 1993). The semelparous and short-lived snail species populations show a more stable phenological pattern than the biennial and pluriennial ones, who mature after the first year of their life, and they are more plastic trying to face the climatic differences from one year to the other.

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Fragmented knowledge on West-European and Iberian Caudofoveata and Solenogastres

Conocimiento fragmentado de los Solenogastros y Caudofoveados de Europa occidental y Península Ibérica

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ABSTRACT

A basic problem in our knowledge of the aplacophoran molluscs, viz. the Caudofoveata and the Solenogastres, is the poor availability of faunistic samplings. This lacunarity even concerns the European waters; in the present contribution, particular attention is paid to the gap in the records along the French and Iberian shelf regions. This is underlined by presenting an updated geographic distribution of eight caudofoveate and thirteen solenogastre species. Benthos investigators are called upon to focus more intensively on sampling the smaller marine fauna from mobile bottoms of the West-European shelf regions.

RESUMEN

Un problema esencial para el conocimiento de los Caudofoveados y Solenogastros (moluscos aplacóforos) es la insignificante disponibilidad de material recogido en diferentes muestreos faunísticos. Esta carencia todavía afecta al Atlántico europeo y particularmente concierne a la falta de muestras en la plataforma continental de Francia y de la Península Ibérica. Esta situación se pone en evidencia con la recopilación actualizada de la distribución geográfica de ocho especies de Caudofoveados y trece de Solenogastros. Se hace una invitación especial a los investigadores del bentos para que intensifiquen su atención por la pequeña fauna marina de sustratos blandos en la plataforma occidental europea.

KEY WORDS: Caudofoveata, Solenogastres, Aplacophora, new records, distribution, Europe.
PALABRAS CLAVE: Caudofoveados, Solenogastros, Aplacophora, nuevas citas, distribución, Europa.

INTRODUCTION

This contribution is restricted to a very simple, but momentous problem: the dearth of faunistic information with all its consequences in both classes of aplacophorous molluscs, the Caudofoveata (formerly Chaetodermomorpha) and the Solenogastres (formerly Neomeniomorpha).

Members of the Caudofoveata and the Solenogastres live predominantly in marine offshore habitats below 50 meters depth and are in general not really rare members of benthic biotopes (see SALVINI-PLAWEN 1990). The Caudofoveata (average size 2-15 mm) are micro-omnivores burrowing within muddy sedi-

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ments, whereas the Cnidaria-vorous Solenogastres (average size 2-20 mm) are bound to clay, secondary hard bottoms or cnidarian colonies. Our scarce knowledge about species diversity, biology and zoogeography of the representatives of both groups is in part due to the intricate, high-effort and expensive sampling methods for benthic meiofauna (ships, cable winches, benthic sledge-dredges). Due to these technical and financial difficulties, investigation of marine meiofauna is generally restricted to the "home turf" of marine biological stations or fishery institutes as typified by Plymouth/UK or Naples/Italy. For more than a century, this has resulted in an unbalanced biogeographic and systematic knowledge of small fauna, even in European waters, restricting the informative data predominantly to animals of the North and Mediterranean Seas. Surprisingly, there are only poor records from the shelf region off France and the Iberian peninsula (delimited in Figure 1 by the 200 m isobath).

Therefore, a special invitation is addressed to all Spanish, Portuguese, and French colleagues who perform benthic offshore investigations to include in their projects the sampling of meiofauna from mobile bottoms. It is only with the help of such cooperative collecting work that examination, determination and research on small benthic animals such as Caudofoveata and Soleno-gastres can be satisfactorily carried out. This cooperation is vital to adequately enlarge our knowledge about the organization, biology and biogeography of these primitive molluscan groups that still bear calcareous bodies instead of a shell. Furthermore, this knowledge is essential to also understand Mollusca in general.

Finally, it must be underlined once more that the determination of members of both classes requires detailed examinations (see SALVINI-PLAWEN, 1975 *versus* ODHNER, 1921, for Caudofoveata; serial sections for most Solenogastres).

The nature of the problem becomes more evident when one examines the concrete documentation. With respect to the presently-known caudofoveate and solenogastre fauna in Northeast-Atlantic (European) waters, there is a distinct gradient between the Scandinavian-British records (cf. SALVINI-PLAWEN, 1975; SEAWARD, 1982, 1991) and the West-European reports. Except for a recent collection from four sites off the coast of Galicia (in connection with the project "Fauna Ibérica"; in preparation), other knowledge of aplacophoran representatives from French and Iberian shelf regions is restricted to a few random findings. On the other hand, investigations and records of both Caudofoveata and Solenogastres are again available from the Mediterranean Sea. For Europe as a whole, this results in an almost "bipolar" pattern of intraspecific distribution. Clearly, in contrast to the regular sampling in Scandinavian, British and Mediterranean seas (cf. SALVINI-PLAWEN, 1972, 1975, 1977a, b, 1988; SEAWARD, 1991), no purposeful offshore samplings have been conducted on the Iberian and French shelf in the past to obtain at least an overview of West-Europe's small benthic fauna including Caudofoveata and Solenogastres (the French BIOGAS and POLYGAS samplings lie beyond the European shelf region).

The overall knowledge on Caudofoveata and Solenogastres has significantly increased during the last decades, but is still very poor when compared with other Mollusca (for an organisational and structural overview see SALVINI-PLAWEN, 1985b, and SCHELTEMA, TSCHERKASSKY AND KUZIRIAN, 1994, respectively; their phylogenetic status is analysed in SALVINI-PLAWEN AND STEINER, 1996). The poor, random information on their occurrence in West-European waters also negatively affects our knowledge on the full range of organisation (systematics, comparative anatomy) as well as on biological conditions and circumstances.

The above-mentioned "bipolarity" in intraspecific distribution, with the intervening West-European gap, becomes obvious when considering all aplacophoran representatives known from both northern and southern waters; these are documented below. Other species with an up to now purely Mediterranean or North-European distribution have a potential West-European occurrence (Lusi-

Figure 1. Section of the West-European Atlantic demonstrating the off-shore shelf region down to the 200 m isobath (followed by the continental decline to 3000 m depth).
Figura 1. Sección del Atlántico europeo mostrando la zona de la plataforma continental, hasta la isóbata de 200 m (seguida de la zona del talud continental hasta los 3000 m de profundidad).

tanic region and / or Bay of Biscay); examples given below are the caudofoveates *Psilodens tenuis* and *Chaetoderma strigisquamatum* as well as the solenogastres *Biserramenia psammobionta* and *Anamenia gorgonophila.*

CAUDOFOVEATA

The Caudofoveata burrow within mobile bottoms and have adapted a vermiform body with reduced pedal sole (midventral fusion of the lateral mantle rims). Generally, sampling in muddy biotopes (sledge-dredges, grabs) success-

fully yields specimens. This group (formerly Chatodermomorpha) was separated from the Solenogastres and elevated to class rank due to the paraphyletic status of its aplacophorous organisation (see SALVINI-PLAWEN AND STEINER, 1996). It includes 98 named species classified into three families (Limifossoridae, Prochaetodermatidae, Chaetodermatidae). Seventeen European representatives have been described so far, six of which occur in the Mediterranean including three endemic species (cf. SALVINI-PLAWEN, 1990).

All species of the West-European shelf region along with the Iberian waters of the Mediterranean will be documented. Thus, among the Prochaetodermatidae, the deep-sea species *Prochaetoderma yongei* Scheltema, *P. clenchi* (Scheltema), and *P. (Chevroderma) turnerae* (Scheltema) from the BIOGAS-cruises are not considered. These three species also inhabit the basin of the Bay of Biscay (2° 10′ - 9° W) at depths of 1175-2006 m (*P. yongei*), 1913-2430 m (*P. clenchi*) and 2124-4760 m (*P. turnerae*) (see SCHELTEMA, 1985; for taxonomy cf. SALVINI-PLAWEN, 1992).

Besides *Falcidens aequabilis*, other species of *Falcidens* (Chaetodermatidae) are likewise of biogeographical interest: at least among the known species which are provided with a slender, tail-like posterior body, each appears to inhabit a well-defined, non-overlapping geographic region. Thus, *F. gutturosus* (Kowalevsky, 1901) is Mediterranean (endemic), while *F. crossotus* Salvini-Plawen has a Scandinavian-British distribution. A third "tailed" species, *Falcidens vasconiensis* Salvini-Plawen, comes from the Gulf of Gascogne (SALVINI-PLAWEN, 1996), and future (not yet recorded) Lusitanic representatives may well belong to yet another species.

Family LIMIFOSSORIDAE

Scutopus ventrolineatus Salvini-Plawen, 1968

Known distribution (Figure 2A): Scandinavian coast (Skagerrak to Tromsö), North Sea, West-Scotland, Irish Sea, southern Bay of Biscaya, Alborán Sea (off Vélez-Málaga), Gulf of Lion (off Banyuls, off Marseille), SE Africa (off Durban); 40-1248 m.

Remarks: The occurrence of this very slender and often coiled species has been summarised in SALVINI-PLAWEN (1975, 1977b). Supplementary records come from the North Sea (Hartley, 1984) and from off Barcelona/Catalonia with the cruises RETRO I (41° 08′ 07″ N, 02° 04′ 32″ E, 510 m) and ESPERMA 89 (41° 04′ 37″ N, 01° 59′ 33″ E, 600 m) carried out by Luis Dantart; a recent finding comes from off Vélez-Málaga (4° 03′ W) at 400 m. This species is of special interest insofar as it has also been recorded from off Southeast Africa, which indicates a distribution along all East-Atlantic.

Scutopus robustus Salvini-Plawen, 1970

Known distribution (Fig. 2B): Off the Norwegian coast with larger gaps from Oslofjord to North of Trondheimsfjord, scattered in the Western Mediterranean Sea to 9° East; 50-3542 m.

Remarks: There are no additional records referring to this slender, up to 10 mm species beyond the occurrence summarised in SALVINI-PLAWEN (1975, 1977a).

Psilodens tenuis Salvini-Plawen, 1977

Known distribution (Fig. 2C): Lusitanic Atlantic S of Cap São Vicente; 2500 m.

Remarks: There is a single record only, as communicated in SALVINI-PLAWEN (1977a).

Family Prochaetodermatidae

Prochaetoderma raduliferum (Kowalevsky, 1901)

Chaetoderma radulifera Kowalevsky, 1901, *Archs. Zool. exp. gén.*, sér. 3, 9: 264.

Known distribution: Endemic in the Mediterranean Sea, known from the Sea of Marmara in the East to off the Algerian coast in the West; 30-2415 m.

Remarks: To date, this species is known only from the Mediterra-nean Sea (see map Abb. 5 in Salvini-Plawen, 1977b). Unlike most other members of the Prochaetodermatidae, *P. raduliferum* is not a true deep-sea species. As is demonstrated by Adriatic and Ionic samplings (30-215 m) as well as by records from off Banyuls (60-275 m) summarised in Salvini-Plawen (1977b), it is quite regularly found on muddy offshore bottoms. In accordance with this, there are new records from off the West coast of Malta at 120-160 m (Mifsud, 1996; the specimen photographed by Mifsud Fig. 2, however, is a broken *Falcidens gutturosus*, see below), from off Barcelona / Catalonia by Luis Dantart (four stations at 41° 04′ 37″-41° 09′ 06″ N, 01° 59′ 33″-02° 07′ 11″ E, 350-680 m), and most recently from off Vélez-Málaga to off Málaga (80-300 m).

Family Chaetodermatidae

Falcidens gutturosus (Kowalevsky, 1901)

Chaetoderma gutturosum Kowalevsky, 1901, *Archs. Zool. exp. gén.*, sér. 3, 9: 281.

Known distribution: Endemic in the Mediterranean Sea, known from off Palestine and from the Sea of Marmara in the East to off Málaga in the West; 40-866 m.

Remarks: *Falcidens gutturosus* is a fairly common species characterised by a slender, tail-like posterior body with an orange-red terminal tassle. Beyond the already known, purely Mediterranean distribution (see map Abb. 2 in Salvini-Plawen, 1977b), there are new samplings from off the West coast of Malta at 120-160 m (Mifsud, 1994, 1996), by L. Dantart from off Barcelona (see Salvini-Plawen, 1996) and by A. Zenetos from the Gulf of Korinth as well as from the Gulf of Petalión (56 m; Greece); most recently, specimens were recorded from off Vélez Málaga (40 m) and off Málaga (211 m).

Falcidens vasconiensis Salvini-Plawen, 1996

Known distribution: Gulf of Gascogne; 141-170 m.

Remaks: Up to present there is a single record only from off the Cap Breton in the southeastern Bay or Biscaya (Salvini-Plawen, 1996). Its distribution throughout the shelf region of the Gulf of Gascogne is to be expected.

Falcidens aequabilis Salvini-Plawen, 1972

Known distribution: Endemic in the Mediterranean Sea, ranging from the Aegean Sea to the western Mediterranean deep-sea bottom as far as the Greenwich meridian; 132-3542 m.

Remarks: This species appears to inhabit deeper and / or far offshore bottoms. Because of the technical effort involved, it is consequently less frequently recorded than *F. gutturosus* or

Prochaetoderma raduliferum, but is well-documented from the West-Mediterranean deep-sea (Campagne Polymède, cf. Salvini-Plawen, 1977a and 1977b: map Abb. 2). There is a new record by Luis Dantart from off Barcelona/Catalonia (RETRO I: 41° 09′ 06″ N, 02° 03′ 54″ E, 350-426 m).

Chaetoderma (?) strigisquamatum Salvini-Plawen, 1977

Known distribution (Fig. 2C): Basin of Alborán (W-Mediterranean Sea); 1491 m.

Remarks: There is a single record of this chaetodermatid species, whose generic classification needs confirmation (radula apparatus; cf. Salvini-Plawen, 1977a). Based on the known distribution of Caudofoveata in the Mediterranean Sea in general (Salvini-Plawen, 1977b), a Lusitanic occurrence of this species might be expected.

SOLENOGASTRES

The Solenogastres (= "those with a belly furrow") include narrowed aplacophoran molluscs that still bear a pedal groove to glide upon (formerly Neomeniomorpha). A total of some 190 species has been described which, in accordance with integumentary characters, is grouped into four orders (Pholidoskepia, Neomeniamorpha, Sterrofustia, Cavibelonia). To date, 46 species are known in European waters, of which 26 (including 19 "endemics") are represented in the Mediterranean Sea. However, little is known about their biogeography: most species have been recorded only once, and inaccurate descriptions (see e. g. *Wirenia*, below) additionally contribute to difficulties in classification, resulting in insufficient faunistic information. Thus, the poorly described *Nematomenia (?) corallophila* (Kowalevsky, 1881), recorded from off La Calle/Algeria at 73-183 m (37° N, 8° 30′ E) as living epizoically on *Corallium rubrum* (Linné), could only be recognised in the future and re-described if it is rediscovered again on a red coral (its alledged finding in the Bay of Rosas/Costa Brava is a mistranslation by Mars, 1965, from Maluquer, 1917).

Most species documented here, together with a few others, belong to the small number of representatives found several times. Records of these findings are very much tied to sampling methods and habitat. For example, the well-known *Neomenia carinata* was never recorded by means of sledge-dredges (muddy bottoms), as predominantly used by the author and his group. In another example, those Solenogastres living on thecaphoran Hydrozoa or Octocorallia (e. g. *Nematomenia* and *Anamenia*, below), are more often sampled from secondary hard bottoms (e. g. with Agassiz-trawls) or by workers studying cnidarians. Thus, all these circumstances help explain our fragmented biogeographic knowledge.

Order Pholidoskepia
Family Dondersiidae

Nematomenia flavens (Pruvot, 1890)

Dondersia flavens Pruvot, 1890, *Archs. Zool. ex. gén.*, sér. 2, 8: XXII.

Known distribution (Fig. 2D): Off Banyuls - Costa Brava, Shetland Islands; 45-167 m.

Remarks: This slender, up to 4 cm long species has a showy lemon-yellow colour. It is not rare along the

rocky (French and Spanish) Catalan coast, feeding upon Hydrozoa-Thecaphora at 45-90 m (PRUVOT, 1891; MALUQUER, 1917; MARS, 1965). Another record refers to the Shetland Islands at 167 m, epizoic upon *Lafoea dumosa* SARS; the anatomical examination revealed the presence of a vestigial radula and the necessity for a family reclassification (SALVINI-PLAWEN, 1978: 39-40).

Recently, the Irish Sea Survey (MACKIE, OLIVER AND REES, 1995: 192) collected eleven samples of *N. banyulensis* (see below); however, there is no information about the exact methos of determination applied. The sampled material had been fixed in formalin and then preserved in alcohol (MACKIE ET AL., 1995: 15-16); the specific body-colour of both *N. banyulensis* (red) and *N. flavens* (yellow) is no longer visible after such treatment. Therefore, it might well be that some of the *N. banyulensis*-records in reality belong to the externally very similar *N. flavens*. Only an accurate histological determination (serial sections) can provide the exact specific classification of these specimens.

Nematomenia banyulensis (Pruvot, 1890)

Dondersia banyulensis Pruvot, 1890, *Archs. Zool. ex. gén.*, sér. 2, 8: XXII.
Nematomenia banyulensis var. *norvegica* Odhner, 1921, *Bergens Mus. Aarb. 1918-19, Naturvid. række* 3: 43.
Myzomenia Simroth, 1893, *Zeitschr. wiss. Zool.*, 56: 324.

Known distribution (Fig. 2E): 0ff Dalmatia, Gulfs of Naples and Salerno, Côte Vermeille, off Roscoff, Plymouth Sound to Irish Sea to W-Scotland, off Northumberland, Trondheimsfjord-Fill (an)fjord; 31-300 m.

Remarks: This well-known species likewise lives epizoically upon Hydrozoa-Thecaphora. Its slender body reaches a length of up to 3 cm and is red (as are also two other Mediterranean species). Its distribution is summarised in NIERSTRASZ AND STORK (1940) and more recently in SEAWARD (1982, 1991) for the British waters. It has also recently been found several times by the Irish Sea Survey (MACKIE ET AL., 1995: 192), but compare the above remarks with *N. flavens*. Geographically new records include samples from off Sebenico/Sibenik (Adriatic Sea) at 57 m, 61 m and 67-68 m (see also SALVINI-PLAWEN, 1986) and from the Fill (an)fjord = north-eastern Hitra Island off Trondheimsfjord (Mus. Uppsala).

A comparative examination of Mediterranean and Norwegian (syntype) individuals, particularly with respect to the mantle scales, revealed no differences which would vindicate a separation of the Norwegian specimens (as variation or subspecies proper).

Stylomenia salvatori Pruvot, 1899

Known distribution: Off Banyuls, (?)Costa Brava; about 60-80 m.

Remarks: This species had been found together with *Rhopalomenia aglaopheniae* (q. v.) in an aquarium filled with benthic material from off Banyuls-sur-Mer; based on the presence of *Rh. aglaopheniae*, this indicates an original depth of about 60-80 m (see PRUVOT, 1891: 721). MALUQUER (1916: 244, 1917: 37-38) reports finding animals similar to *S. salvatori* from the Bay of Rosas and off Llansà (Costa Brava). Even if the occurrence of this species is to be expected there, the record needs to be confirmed because no accurate determination (histological examination) was performed.

Family Lepidomeniidae

Tegulaherpia myodoryata Salvini-Plawen, 1988

"Species D" in Salvini-Plawen, 1968a, *Sarsia*, 31: 132.
Tegulaherpia celtica Caudwell, Jones and Killeen, 1995, *Journ. Conch. (London)*, 35: 258.

Known distribution (Fig. 2F): Off Livorno, off Banyuls-sur-Mer, southern Bay of Biscay (North of Asturias, THALASSA-Stat. W-415)?, Celtic Sea, area around Bergen (Raunefjord, Hjeltefjord), area around Trondheim (Fill (an)fjord, Trondheimsfjord); 75-470 (75-860/1150?) m.

Remarks: This Mediterranean species is likewise native to Northern Europe. In the course of examining more comprehensive Solenogastres material from the North Atlantic, the already communicated "Species D" (Salvini-Plawen, 1968a) and *T. celtica* (Caudwell, Jones and Killeen, 1995), according to histological examination by series sections, turned out to be conspecific with *T. myodoryata* from the Western Mediterranean Sea as described in Salvini-Plawen (1988). Moreover, several other Norwegian individuals (Hjeltefjord, 200 m; Fill (an)-fjord, Trondheimfjord, 470 m) likewise belong to this species.

A single specimen from the THALASSA-Cruise (Stat. W-415, 43° 55′ 06″ N, 06° 11′ 18″ W; 860-1150 m), forwarded in 1971 by F. Monniot (Paris) to the author, possibly also represents *T. myodoryata*, since the mantle scales fully fit into the range of shape, outline and size of the *myodoryata*-scales. However, the animal was useless for histological examination, and the record from a depth between 860 and 1150 m lends doubt to a conspecificity as long as no bathymetrically interbridging and/or additional samples are taken.

Family Wireniidae

Wirenia argentea Odhner, 1921

Aesthoherpia glandulosa Salvini-Plawen, 1985, *The Mollusca* (Academic Press), 10: 94.
"Species B" in Salvini-Plawen, 1968a, *Sarsia*, 31: 131.
Aesthoherpia glandulosa Salvini-Plawen and "Species D" Haszprunar, 1986, *Zool. Anz.*, 217: 345-360.

Known distribution (Fig. 3A): Area around Bergen/Norway, Hardangerfjord, area of Trondheimsfjord, Adriatic Sea, Aegean Sea; 95-700 m.

Remarks: A most recent examination of the hitherto missing type material of *Wirenia argentea* Odhner (now in the Naturhistoriska Rijkmuseet, Stockholm) revealed that *Aesthoherpia glandulosa* Salvini-Plawen is conspecific with it. Despite some inaccurate and insufficient presentations by Odhner (1921: 31-34; foregut, no radula, and so on), which led to the description of *Aesthoherpia* (see Salvini-Plawen, 1988: 383-384), *Wirenia* has nomenclatorial priority. The organisation of the species and its presently known geographic distribution are communicated (as *Aesthoherpia glandulosa*) in Salvini-Plawen (1988). Some additional findings come from recently examined Norwegian samples: area Northwest of Bergen (Hjeltefjord, 280 m; Herdlafjord, 200 m; Mangerfjord, 350 m) and Fill (an)fjord-Trondheimsfjord (95 m, 185 m, 320 m, 470 m and 490-500 m). The record of "*Wirenia argentea*" by Hartley (1984) from the North Sea needs specific confirmation.

Family Macellomeniidae

Macellomenia palifera (Pruvot, 1890)

Paramenia palifera Pruvot, 1890, *Archs. Zool. exp. gén.*, sér. 2, 8: XXIII.

Figure 2. A-C. Caudofoveata. Known European distribution. A: *Scutopus ventrolineatus* Salvini-Plawen, 1968; B: *Scutopus robustus* Salvini-Plawen, 1970; C: Known records of *Psilodens tenuis* Salvini-Plawen, 1970 (black circle) and of *Chaetoderma(?) strigisquamatum* Salvini-Plawen, 1971 (asterisk). D-F: Solenogastres. Known distribution. D: *Nematomenia flavens* (Pruvot, 1890); E: *Nematomenia banyulensis* (Pruvot, 1890); F: *Tegulaherpia myodoryata* Salvini-Plawen, 1988.

Figura 2. A-C. Caudofoveados. Distribuciones conocidas. A: Scutopus ventrolineatus *Salvini-Plawen, 1968; B:* Scutopus robustus *Salvini-Plawen, 1970; C: Citas conocidas de* Psilodens tenuis *Salvini-Plawen, 1970 (círculo negro) y de* Chaetoderma(?) strigisquamatum *Salvini-Plawen, 1971 (asterisco). D-F: Solenogastros. Distribuciones conocidas. D:* Nematomenia flavens *(Pruvot, 1890); E:* Nematomenia banyulensis *(Pruvot, 1890); F:* Tegulaherpia myodoryata *Salvini-Plawen, 1988.*

Known distribution (Fig. 3B): Côte Vermeille, Irish Sea (?); 80-120 m.

Remarks: This species, with its particular calcareous mantle-bodies, was originally recorded with a single specimen North of Port Vendres (Côte Vermeille; southeastern France) on muddy bottom at 80 m. Two individuals recently sampled from the Irish Sea at 80 m and 120 m come very close to *M. palifera* (CAUDWELL *ET AL.*, 1995). In view of the "bipolar" occurrence of other species (demonstrated herein), there is a high probability that the species are identical. However, as the British animals have not been investigated anatomically (series sections), true conspecificity ramains uncertain.

Order NEOMENIAMORPHA

Family NEOMENIIDAE

Neomenia carinata Tullberg, 1875

Solenopus nitidulus Koren and Danielssen, 1877, *Arch. Math. Naturvid. (Kristiania)*, 2: 124.
Solenopus affinis Koren and Danielssen, 1877, *Arch. Math. Naturvid. (Kristiania)*, 2: 127.
Neomenia grandis Thiele, 1894, *Zeitschr. wiss. Zool.*, 58: 223.

Known distribution (Fig. 3C): Northern Kattegat and Bohuslän (W-Sweden), Norwegian coast between Oslofjord and Sognesjöen/Sogne-fjord, Romsdalsfjord, Trondheimsfjord, South of Lofoten, Iceland, Shetland Islands, British Isles, off Roscoff, Costa Brava, Gulf of Genova, Gulf of Naples, off Messina; 10-565 m.

Remarks: This up to 3 cm long species has a stoutish shape and is well documented along the coast of Scandinavia and around the British Isles (KOREN AND DANIELSSEN, 1879; WIRÉN, 1892; ODHNER, 1921; MUUS, 1959; SEAWARD, 1982, 1991) including Strindfjord/ Trondheimsfjord (Mus. Copenhagen) and the Hebrides (Mus. Leiden). The Mediterranean records include *N. affinis* (Koren and Danielssen) which, according to certain, minor anatomical differences (pers. obs.), can be classified as a subspecies only (SALVINI-PLAWEN 1986); the same holds true for *N. grandis* Thiele (NIERSTRASZ AND STORK, 1940). A remarkable record refers to Iceland (KNUDSEN, 1949), a region in which *Neomenia dalyelli* (Koren and Danielssen) is generally found.

Order CAVIBELONIA

Family PARARRHOPALIIDAE

Eleutheromenia sierra (Pruvot, 1890)

Paramenia sierra Pruvot, 1890, *Archs. Zool. exp. gén.*, 8: XXIII.

Known distribution (Fig. 3D): Costa Brava, Bretagne; Irish Sea; Trondheim region; 40-128 m.

Remarks: PRUVOT (1891) typifies the species from a single specimen (Cap Creus/Costa Brava; 80 m) and in 1897 he reports another finding from off Roscoff at about 40 m (PRUVOT, 1897). A single specimen of typical appearence (lobed dorsomedian keel) from Stjörn (North or Trondheim/Norway), despite the geographical distance, after serial section revealed to be *Eleutheromenia* sierra. Consequently, the questioned presence or this species in the southwestern Cartigan Bay (Irish Sea, 52 m; see HARTLEY 1984, SEAWARD, 1991: 14) as well as the specimens from nine samples or the Irish Sea Survey referred to *E. sierra* (CAUDWELL *ET AL.*, 1995: 266; MACKIE *ET AL.*, 1995: 192; not documented in Fig. 3D) are indirectly confirmed to really belong to this species.

On the other hand, the Pararrhopaliidae represent a fairly diverse group of sys-

Figure 3. Solenogastres. A: Known distribution of *Wirenia argentea* Odhner, 1921; B: Records of *Macellomenia palifera* (Pruvot, 1890) (black circles) and of *Meromenia hirondellei* Leloup, 1949 (asterisk); C: Known distribution of *Neomenia carinata* Tullberg, 1875; D: Records of *Eleutheromenia sierra* (Pruvot, 1890), see text; E: Known distribution of *Biserramenia psammobionta* Salvini-Plawen, 1968; F: Known European distribution of *Rhopalomenia aglaopheniae* (Kowalevsky and Marion, 1887).
Figura 3. Solenogastros. A: Distribución conocida de Wirenia argentea *Odhner, 1921; B: Citas de* Macellomenia palifera *(Pruvot, 1890) (círculos negros) y de* Meromenia hirondellei *Leloup, 1949 (asterisco); C: Distribución conocida de* Neomenia carinata *Tullberg, 1875; D: Citas de* Eleutheromenia sierra *(Pruvot, 1890), véase texto; E: Distribución conocida de* Biserramenia psammobionta *Salvini-Plawen, 1968; F: Distribución europea de* Rhopalomenia aglaopheniae *(Kowalevsky y Marion, 1887).*

tematically very difficult representatives (see SALVINI-PLAWEN, 1978); several geographically close records of Pararrhopaliidae may represent different species (or even genera). Thus, another record from the Irish Sea (*Pruvotina* sp. in CAUDWELL *ET AL.*, 1995: 265-267) clearly does not belong to *E. sierra*; the same can be said about two THALASSA-specimens from off Galicia and off Asturias (Bay of Biscay)

Family SIMROTHIELLIDAE

Biserramenia psammobionta Salvini-Plawen, 1968

Known distribution (Fig. 3E): Irish Sea, Plymouth area, Bretagne, Galicia; 8-30 m.

Remarks: In addition to the type material from off Roscoff at 8-10 m (SALVINI-PLAWEN, 1968b; see also MONNIOT, 1965), several individuals have recently been recorded in Plymouth Sound at 9-11 m (50° 20′ 43″ N, 4° 09′ 05″ W; see also KIKINGER AND SALVINI-PLAWEN, 1995). Moreover, a single specimen has been sampled by Ian Killeen during the Irish Sea Survey from the Cardigan Bay/Wales (Stat. 46, 52° 19′ 12″ N, 04° 37′ W) at 30 m, provided by Cathy Caudwell to the author (see also CAUDWELL *ET AL.*, 1995). Finally, the 12 Solenogastres referred to as "*Lepidomenia* sp." by Celia Besteiro in her Ph. D. thesis (1986) from Galicia/Spain (Ría de Ferrol, "Bajo de la Palma"; 43° 27′ 59″ N, 08° 16′ 23″ W; 14 m) also represent *Biserramenia psammobionta*. They all come from coarse sand or shell gravel bottoms and at least those from Roscoff, Plymouth and Galicia are interstitially living animals (cf. SALVINI-PLAWEN, 1985a; also OTT AND BOCHDANSKY, 1991, for the Plymouth animals).

The histological examination of these specimens revealed some details beyond the original description (SALVINI-PLAWEN, 1968b). First, the characteristic circular musculature around the spawning ducts and the posterior mantle cavity is not yet elaborated in juveniles. The slender pericardioducts with a tiny lumen still open from dorsal into the spawning ducts close to their rostral ends, these ducts being paired throughout with a wide lumen. Further differentiation thus includes a curving elongation of the rostral portion of the spawning ducts, which results in the adult spawning ducts bending dorso-posteriorly (as described in 1968). Here, the pericardioducts join their ends not axially but ventrally, thus causing a bulgy enlargement or even a slight bend in the continuous lumen. This bulged enlargement is the site of sperm storage, thus functioning as receptacula seminis; well-defined, set-off seminal pouches (vesiculae seminales, as described earlier), however, are not present. The paired lateral pouch of the ventrorostral mantle cavity is well differentiated only in fully-grown individuals and often merely represents two simply lobulated, more or less distinct sacculations opening medially through a short duct or pore into the pallial space. Rather than being paired in the sense of two singular, separate ganglia, the cerebral ganglia are fused together in the middle third of their extension. In some specimens a small dorsoterminal sense organ could be detected at the rear of the body.

Family AMPHIMENIIDAE

Meromenia hirondellei Leloup, 1949

Known distribution (Fig. 3B): Northern Bay of Biscay; 166 m.

Remarks: A single fragment of this species had been recorded from the continental platform in the northern Bay of Biscay (46° 27′ N, 4° 09′ 45″ W) at 166 m depth. Due to the unknown organisation of the anterior body, the generic classification is uncertain (LELOUP, 1950: 21-23; SALVINI-PLAWEN, 1972: 224-225).

Figure 4. Solenogastres. A: Known European distribution of *Anamenia gorgonophila* (Kowalevsky, 1880); an additional record refers to the Azores; B: Known distribution of *Dorymenia sarsii* (Koren and Danielssen, 1877).

Figura 4. Solenogastros. A: Distribución europea de Anamenia gorgonophila *(Kowalevsky, 1880); una cita adiccional se refiere a las islas Azores; B: Distribución conocida de* Dorymenia sarsii *(Koren y Danielssen, 1877).*

Family RHOPALOMENIIDAE

Rhopalomenia aglaopheniae (Kowalevsky and Marion, 1887)

Rhopalomenia eisigi Thiele, 1894, *Zeitschr. wiss. Zool.*, 58: 269.

Known distribution (Fig. 3F): Off Cap Matapan / Tainaron (South-Peleponnes), Gulf of Naples, off Marseille, Côte Vermeille, off Roscoff, British Isles; 50-137 m.

Remarks: This well-known species lives upon Hydrozoa-Thecaphora, almost exclusively upon *Lytocarpia myriophyllum* (Linné). The distribution is compiled in NIERSTRASZ AND STORK (1940), SALVINI-PLAWEN (1972) and SEAWARD (1982, 1991). The identification of several specimens from off Monrovia / Liberia (THIELE, 1906: 324) needs re-examination and / or confirmation.

Family STROPHMENIIDAE

Anamenia gorgonophila (Kowalevsky, 1880)

Proneomenia nierstraszi Stork [in Nierstrasz and Stork], 1940, *Zoologica (Stuttgart)*, 99: 57.
Anamenia heathi Leloup, 1947, *Bull. Mus. roy. Hist. Nat. Belgique*, 23 (26): 1-11.

Known distribution (Fig. 4A): Gulfs of Naples and Salerno, off La Calle (easternmost Algeria), off Marseille, Sea of Alborán, Gorringe-Bank (WSW of Cap São Vicente), Azores; 65-845 m.

Remarks: The records of this species have been revised by SALVINI-PLAWEN (1972). The investigation of numerous Solenogastres recorded more recently from the SW of the Isle of Alborán (see TEMPLADO, GARCÍA-CARRASCOSA, BARATECH, CAPACCIONI, JUAN, LÓPEZ-IBOR, SILVESTRE AND MASSÓ, 1986: 101-102) revealed that they in part belong to *A. gorgonophila*, and the known distribution of the species supports the assumption of its presence in Lusitanian waters as well. This species lives upon Gorgonaria, predominantly upon *Paramuricaea clavata* (Risso) = *P. chamaeleon* (Koch), but also upon *Eunicella* spp. and others.

Family Proneomeniidae

Dorymenia sarsii (Koren and Danielssen, 1877)

Simrothiella sarsi Auctt. (see Opinion 1185 ICZN)

Known distribution (Fig. 4B): Trondheimfjord, Sognefjord, Bergen area, Oslofjord, Skagerrak, Gorringe Bank (off Cap Sao Vicente); North Atlantic-Arctic Ocean outside Tromsö?; 183-681 m (1134 m?).

Remarks: The up to 7 cm long, slender species was redescribed by Odhner (1921) and is externally characterised by a distinct (dorso-)terminal extension of the body; a photograph is given in Salvini-Plawen (1968a: Abb. 23). Some recently examined material from Scandinavian collections extends the known distribution (see Fig. 4B); the North Atlantic-Arctic specimens (71° 25′ N, 15° 41′ E, 1134 m; see Odhner, 1921, and Jaeckel, 1954) only doubtfully belong to *D. sarsii* based on the geographic and bathymetric distribution. In addition to the polystichous radula, a pair of copulatory stylets and the presence of a dorsoterminal sense organ typical for the genus, histological investigations underline two particular specific characters in mature animals: the anterior portion of the pericardioducts bears small pockets serving as vesiculae seminales, and the posterior portion of the spawning ducts ("lower gametoducts") in front of their fusion each elaborate a ventral enlargement or voluminous sacculation (pocket). Both these characters allow this particular *Dorymenia* species to be identified in Scheltema *et al.* (1994: Figs. 22 E and 24 G) as *D. sarsii* (Koren and Danielssen). The geographic distribution of this species is thus enlarged to the Gorringe Bank of the Iberian shelf region (36° 50′ N, 9° 15′ W, 681 m; cf. Scheltema *et al.*, 1994: 18).

Family Lepidomeniidae

Lepidomenia ? spp.

Lepidomenia hystrix Auctt. non Marion and Kowalevsky, 1886
Lepidomenia (?) swedmarki Salvini-Plawen, 1985, *Stygologia*, 1 (1): 103.

Remarks: Some records of small, mesopsammic Solenogastres from off Marseille, Bretagne and off Belfast / Northern Ireland have been systematised as *Lepidomenia hystrix* Marion and Kowalevsky (see Salvini-Plawen, 1985a; Seaward, 1991). Referring to the discussion in Salvini-Plawen (1985a), the classification of these animals (not having been investigated anatomically) as *L. hystrix* is unwarranted and misleading. The specimens should be determined by means of serial sections rather than simply naming them based on accessory features.

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Molluscs as evolving constructions: necessary aspects for a discussion of their phylogeny

Los moluscos como construcciones en evolución: aspectos necesarios para una discusión sobre su filogenia

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ABSTRACT

A model for the evolution of molluscs is presented. The reconstruction is based on the Frankfurt Theory which conceives organisms as energy transforming hydraulic units which are subject to evolutionary transformation according to the constructional principles ruling organisation. Evolution is reconstructed as a process of constructional transformations in which all stages are explained as explicitly viable constructions; the irreversible transformation phases are also rationally explained by referring to constructional properties of the organismic machines. It is maintained that the predecessors of molluscs must have been elongate worm like animals which were internally tethered by muscles in a way that creeping on the flattened ventral "foot" surface became possible. Only organisms controlling the cross-section by a densely spaced muscle system could start creeping on hard substrate. The establishment of the radula is shown to have been dependent on the adhesive creeping movements which allowed anchorage of the construction to the substrate during rasping. The formation of the shell elements was rendered possible by concentration of motility to the ventral side while the dorsal body wall was held undeformed as a precondition for shell formation. Formation of the muscle grid of the foot on the ventral side of the body and the stabilisation by skeletal elements of the dorsal side caused a shift of the inner organs into a dorsal hump. From the model for the primitive molluscs with segmented shells the continuation into the conchiferan constructions with fused shells and the constructional lineages into the major mollusc constructions are given in captions parallelizing sequences of visualisations of the constructional stages with the major alterations.

RESUMEN

Se presenta un modelo sobre la evolución de los moluscos basado en la Teoría de Frankfurt, que concibe a los organismos como unidades hidráulicas transformadoras de energía sujetas a transformaciones evolutivas de acuerdo con los principios constructivos que regulan la organización. La evolución se reconstruye como un proceso de transformaciones construccionales en el que todos los estados se explican como construcciones explícitamente viables; las fases de transformación irreversibles también se explican racionalmente refiriéndolas a propiedades construccionales de las máquinas orgánicas.

Se defiende que los predecesores de los moluscos deben haber sido animales alargados, tipo gusano, que contaban con una malla muscular interna de tal manera que fuese posible arrastrarse sobre la superficie aplanada ventral del "pie". Sólo aquellos organismos que controlasen su sección mediante un sistema muscular densamente espaciado podían empezar a arrastrarse sobre un sustrato duro.

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La aparición de la rádula se muestra como un proceso dependiente de los movimientos de reptación que permitieron el anclaje de la estructura al sustrato durante el raspado. La formación de elementos conchíferos fue posible por la concentración de la motilidad en la cara ventral mientras que la pared dorsal del cuerpo se mantenía sin deformación, paso previo para la formación de una concha. La aparición de la malla muscular del pie en la cara ventral del cuerpo y la estabilización de la cara dorsal mediante elementos esqueléticos provocaron el traslado de los órganos internos hacia una joroba dorsal. A partir del modelo de moluscos primitivos con conchas segmentadas se presenta el desarrollo hacia construcciones conchíferas con conchas fusionadas y hacia las principales estructuras construccionales de moluscos, mediante encabezamientos de sequencias paralelas de estados de desarrollo, incluyendo las principales alteraciones.

KEY WORDS: Molluscs, hydraulic constructions, phylogenetical reconstruction, metamery, radiation.
PALABRAS CLAVE: moluscos, construcciones hidráulicas, reconstrucción filogenética, metamería, radiación.

INTRODUCTION

Evolution can never be directly observed. It must be reconstructed in models describing the sequences of transformational steps. All stages of evolution necessarily have to be represented by explicitly viable organismic constructions. The theoretical concept and the methodology which allows such reconstructions is the Frankfurt Evolution Theory (FET) (Gutmann, 1974, 1989; Bonik, Grasshoff and Gutmann, 1977; Gutmann and Edlinger, 1994a, b, c, d; Edlinger, 1989a, b; Edlinger, Gutmann and Weingarten, 1991; Vogel, 1991). In accordance with the demands and results of other biological disciplines, this theory conceives of organisms as energy transforming units and as autoformative constructions. Reconstructions of the evolutionary changes in the sense of the Frankfurt Evolutionary Theory are supported by the insight into the constructional properties of all animal soft body systems which function as hydroskeleton apparatuses and hydraulic units. Before reconstructions are attempted the principles and physical laws governing the organismic entities must be known.

ORGANISMS: ENERGY TRANSFORMING ENTITIES

On the basis of constructional explanations metazoan animals must be described and explained as self-sustaining and energy transforming systems. Basically, they function as machines. They are capable of actively acquiring matter and energy from their environment. By transforming the chemical energy thus obtained into mechanical force the working activity of the body construction is generated.

Energy transformation in the constructions is determined by the structure of specific macromolecular components, mainly in muscles and cilia. To become effective as driving engines the energy transforming structures have to be integrated into an energy cascade of a mechanically coherent structural whole in which the forces are transmitted to mechanically working units. A chain of force transmitting structures connects the energy transforming sites with the working units of the animal body. This chain must never be interrupted because interruption would lead to dysfunction and failure of the organismic construction. The internal activity is also dependent on the form determining structural order and on the effective suppression of useless motoric deformations by restraining structures.

After the chemo-mechanical energy transformation on the macromolecular level the energy is finally utilised in the machinery for the generation of form, locomotion, behaviour, and also for reproduction.

The constructional concept of organisation conceives of organismic units as hydraulic entities that are composed of enclosing membranes and flexible integumental walls. The form of every living body must be enforced by tethering and or bandaging structures which suppress the tendency of all living (hydraulic) units to assume a spherical shape. In animal constructions the form is entirely or mainly determined by the tensile force of muscles and by the mesh of connective tissue structures which are organised in highly ordered arrays. In the course of evolution all transformation stages must be shown to comply with the laws of form-enforcement in hydraulic units. The internal constructional principles and law-like principles determine the directionality and the irreversibility of evolutionary change.

The capability of living constructions to function as energy transforming apparatuses and the ability to obtain an input of matter and energy are determined by the structural order of the energy transforming and working construction. All stages of evolutionary transformation series must never lose their structural order and can only undergo gradual transformation in a way that the preceding constructional stages open up the organismic options of the subsequent alterations. These alterations lead into constructional alleys with further transformation sequences.

Evolution which is driven by the activity of the organisms themselves and the insuppressible generation of non-directional variation has to follow very specific internal principles; the step by step alterations must be forced on alleys of ordered constructions and on sequences of non-fortuitous stages.

Because the principles and laws of organisation can be elucidated in extant organisms, the transitional sequences can be reliably reconstructed. So models can be formulated which are rational in respect to the methodology applied. Consequently they provide valid explanations of the intermediate constructional stages.

In all organismic constructions the course of evolution, mainly of the gross morphological level, can be shown to depend on the constructional organisation outlined above. Consequently all minor physiologically, cytologically, and histologically based functions must be understood as subservient and dependent on the conditions given by the construction as a whole.

Morphological features and so called morphological characters in the traditional sense, at all levels of the organisms, must be seen as enforced by mechanical structures and as energy transforming structures.

Constructional morphology and the reconstruction of evolutionary transformation do not allow the employment of traditional methodologies which prescribe the dismantling and disintegration of living constructions into morphological patterns or an array of distinct characters. Such a procedure is advocated by cladistic "methodologies". Selection and delimitation of features automatically destroys the coherence of organismic systems and the basic hydraulic constitution. In living machines constructional coherence, the hydraulic properties, the order of form-enforcing structures, and the cataract of energy transforming structures of organisms are not accessible to character analysis and comparison of form as advocated by traditional morphology. Only constructional alterations based on the reconstruction of constructionally and functionally viable stages are of interest.

Superficial aspects of similarity of form and so called homologies in the sense of traditional morphology are also of no relevance because constructional explanation has to follow lines of analysis that are comparable to engineering procedures.

Such principles preclude the depiction of fortuitous alterations and arbitrary morphoclines and allow the determination and the reconstruction of the transformation alleys and the establishment of the sequences of stages in the course of evolution. All evolutionary alterations must be shown to be delimited by the internal constructional properties of the living machines (Fig. 1).

Thus, the constructional alterations of evolution have to be reconstructed as

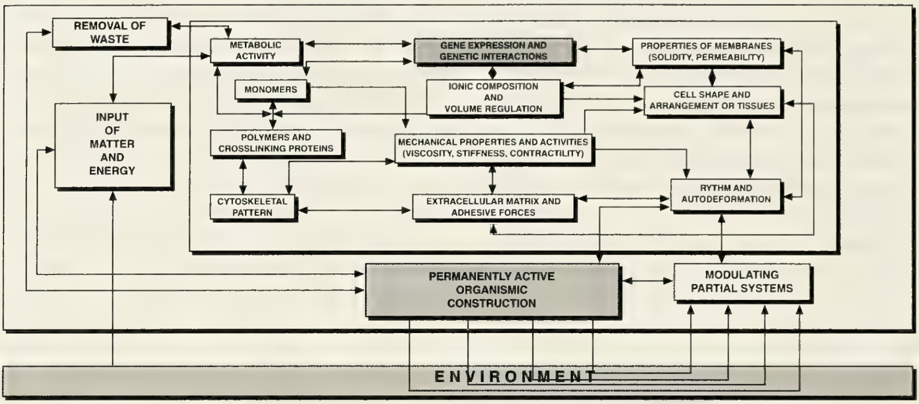

Figure 1. Interrelations between the different levels and parts of organisms and between organisms and their environment (after BEREITER-HAHN, 1991 and EDLINGER, 1995).
Figura 1. Interrelaciones entre los diferentes niveles y partes de organismos y entre los organismos y su medio ambiente (tomado de BEREITER-HAHN, 1991 y EDLINGER, 1995).

internally guided and directed and cannot be understood as adaptational processes or as ruled by environmental factors in the sense of Darwinian thinking. Evolution in the sense of the FET, which is certainly the most radical variant of post-Darwinian concepts assumes a new status and is based on the properties of the evolving organismic entities. Therefore, all Darwinian tenets are excluded from the reconstructions as they are not conducive to the constructional principles which rule organismic constructions and evolutionary transformation.

The theoretical tenets and the methodology of the reconstruction procedures were elaborated by a group of authors (BONIK *ET AL*., 1977; GUTMANN, 1974, 1989; EDLINGER, 1989A, B, 1991a, b, 1992a, b, 1994a, b; EDLINGER *ET AL*., 1991; VOGEL, 1991). Numerous models provide corroborating evidence for the successful application of the methods and for the validity of the non-Darwinian evolutionary theory.

On the basis of the just outlined concept ontogenetic and phylogenetic development of molluscs (like that of other "bauplans" of animals) must be reconstructed as transformational sequence of organismic constructions over viable intermediate constructional forms. The sequence of evolutionary alterations must be ruled by the intrinsic laws and constructional principles which are responsible for the continuation of energy transformation and motoric activity in all stages.

MOLLUSCS AS A CASE STUDY

In the following the evolution of the mollusc constructions is presented as a case study. The stages of mollusc evolution have to be described and figured out as tethered systems which in most cases allow flattening of the foot. In this way they can exert sufficient control of body shape by tethering muscles while the shell structures serve only as deformation suppressing elements in the dorsal parts of the coherent whole.

THE DERIVATION OF THE MOLLUSCS: THE KEY TRANSFORMATION STEPS

In reconstructions based on constructional morphology the morphoclines and all aspects of directionality of evolutionary transformation are derived from the biomechanical princi-

ples of the living organisms. Thereby, the arrow of time is firmly supported by irreversible constructional explanation. On the basis of the constructional analysis only the derivation of molluscs from annelid-like forerunners can be consistently explained (GUTMANN, 1974; EDLINGER, 1991a).

The basic mollusc construction must certainly have been a creeping creature with a flattened foot and a dorsal shell or a sequence of shell elements. The problem posed by this basic and only sketchily figured out construction can be formulated in the following way.

How can such a constructional constitution arise in skeleton free hydraulic forerunners of whatever kind of primitive metazoan organisation? Which constructional organisation might have been the incipient stage for the emergence of the basic properties?

The key changes can only be explained if one sets the starting point of the transformation sequence in an annelid like segmented soft body construction which was capable of controlling the cross-section of the body in a way that creeping on a flattened ventral side became possible. Flattening must have been the first stage of adhesive creeping.

The initiation of creeping on a flattened ventral side was a realistic option of annelid-constructions with an internal tethering by dissepimental and other muscles which traversed the cross section of the elongate apparatus.

In conjunction with the development of the adhesively creeping foot and its anchorage at the substratum the radula developed in a well demarcated head region. The use of the radula as a rasping organ was dependent on the concomitant formation of the adhesive creeping foot apparatus. This apparatus allowed the radula indirectly to be pressed against the substratum during feeding. Simultaneously the shells could come into existence as dorsal stabilising structures in the non deformed dorsal portions of the body, while an intensification of motility for peristaltic adhesive creeping occurred on the ventral side. This constructional constitution is in some way still existing in extant flattened chitons.

After the establishment of this construction with its segmented sequence of skeletal structures in polyplacophoran-like organisms new paths of evolution were viable. They led to worm-like constructions in a step by step loss of the shell. In this way some recent forms of worm-like molluscs, the Ventroplicata and the Caudofoveata, are easily derivable from chiton-like predecessors.

Fusion of the shell-plates occurred in the other major branch. Fusion of the segmented shells, in accordance with specific changes of the soft body led to the formation of the conchiferan construction with its typical unified shell.

One consequence of this fusion of the conchiferan shell was that, in conjunction with the formation of the fused shell, a narrow waist developed between the cephalopodium and the dorsal body portion while the internal organs were restructured in the frame of a visceral hump.

The basic conchiferan organisation is to a certain extent represented in the still extant Tryblidiaceans which display clear metamerism of some organs. The basic Conchiferans provided the constructional basis for a radiative explosion that generated most molluscan construction types of the conchiferan level.

The narrowing waist caused and even enforced reductions especially of the of the number of dorsoventral muscles, gills, and kidneys and the compensatory enlargement of the few persisting organs.

The major steps of transformation are described and depicted in the illustrations. The complete explanation of the transitions leading to the mollusc constructions cannot be presented here. It was elaborated in a sequence of papers which may be consulted by the interested and critical reader. In the following the major steps are depicted in the illustrations. The ensuing explanation is formulated as a caption in respect to the illustration (Fig. 2). It should be stressed that the pictures are no typical morphological illustrations.

They present visualisations of the array of form enforcing structures and have to be conceived as constructional models.

(1.1.) A worm-like predecessor (GUTMANN, 1974; EDLINGER, 1991a) with metameric coelomic pouches, dissepiments, and other segmental tethering elements. Flattening is made possible by dorsoventral and other muscles on the dissepiments. All non-longitudinal muscles are helpful in controlling the cross-section and allow flattening of the worm-like body in the incipient stages of creeping on hard substrate.

Metamerism which allowed flattening of the ventral side of the body is mandatory in the precursor stages of molluscs. Flattening of the body is only possible by internal tethering structures such as muscle bearing dissepiments and internal muscles transcending the coelomic chambers which were capable of suppressing the tendency to assume a circular shape. Lack of cross sectional tethering as observed in non-metameric worms would result in a circular cross-section of the soft body and preclude even the beginning creeping on hard substrate.

In an early stage of evolution the mouth became equipped with chitinous teeth which were located around the stomodeum and in the foregut.

(1.2.) Transition to the basic mollusc construction required the formation of a thick ventral muscle lattice forming a flat and highly deformable foot which was able to follow the contours of the bottom. This enabled the organisms to creep adhesively and start rasping at the substrate.

In the course of the incipient stages of transformation the coelom and the other inner organs were shifted to the dorsal side. In the dorsal part of the animals coelomic metamerism was retained and even further demarcated by the newly developing shells.

(1.3.) As muscular activity in the form of peristaltic waves travelling over the foot was concentrated in the ventral portion of the pre-mollusc constructions the dorsal parts of the body were held mostly undeformed. In this situation serial shell elements developed as economising structures; they replaced energetically expensive structures such as muscles and connective tissue structures. The newly developed skeletal structures served as stabilising elements in the deformable and still worm-like hydraulic apparatus. As the shells formed a sequence of independent elements bending movements of the body were still possible; they are remnants of the worm-like bending and peristaltic activity of the predecessors. The dorsally situated serial plates were mechanically connected to the foot by strong muscles which continue to demarcate the preceding metamerism of the annelid-like predecessors.

In accordance with the mechanical requirements for the flattening of the foot the pairs of muscles were arranged as densely spaced pairs of vertical, transverse, and oblique bundles under each plate. These muscles project into the dense muscular grid of the foot. Transversely oriented muscles cross from one side to the other. In this way the form of the whole animal is under control of the tethering structures. Lateral extensions of the shells and their roof-like position allowed the formation of lateral grooves. In these grooves the metameric gills were established as projections of the soft body wall. They were indispensable for the developing molluscs because the adhesion of the foot to the bottom and the covering dorsal shells reduced the body surface usable for respiration. Only the lateral parts of the soft body continued to be exposed to the surrounding medium. The newly developing gills were forced into the old metameric constellation because the vessels had to pass between the pre-existing metameric muscle bundles.

Around the shell a spicule bearing girdle consisting of connective tissue and musculature was established. This girdle served as a protection for the lateral grooves with the gills.

Pari passu with the rearrangement of the musculature the large coelomic cavities of the annelid like ancestors were restrained to a narrow dorsal strip. While the posterior part of the coelom was altered

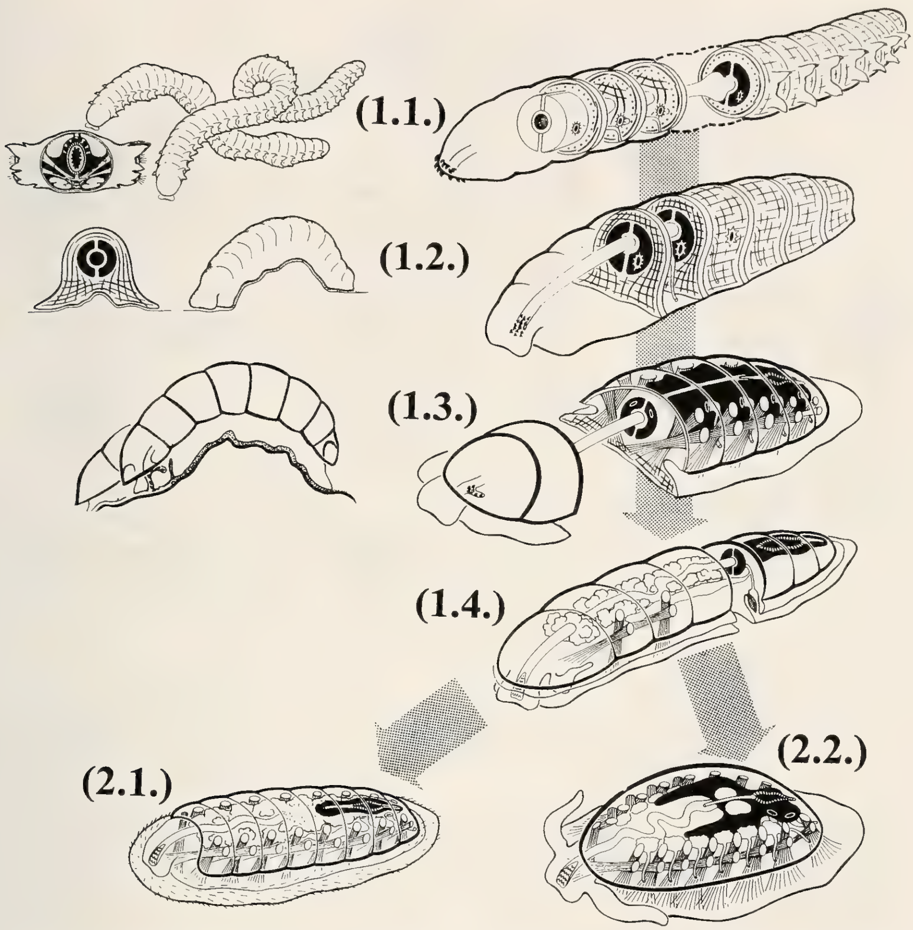

Figure 2. The evolution of chiton-like molluscs out of annelid-like metameric ancestors. An early branching into chiton-like and conchiferan constructions occurs.
Figura 2. Evolución de los moluscos con forma de quitón a partir de ancestros metaméricos tipo anélido. Tiene lugar una pronta separación entre construcciones conchíferas y con forma de quitón.

into the pericardium around the effectively pumping heart the other parts served as cavities containing the gonads.

In conjunction with adhesive creeping the structures around the mouth were perfected into a radula by shifting of the chitinous teeth into a ventral pouch of the foregut. The establishment of the radula must be seen in conjunction with the creeping mode of locomotion. The scraping radula could only become effective when the body remained firmly attached to the substrate in a way that exertion of pressure by the radula onto the substrate would not push the animal body away from the underlying surface. From this follows that the radula could only develop in strict interdependence with the creeping performance of the foot.

(1.4.) Reconstructed predecessors of Conchiferan and Polyplacophoran constructions. In the anterior portion of the body the coelom was gradually reduced. The gut formed lateral pouches in the form of the midgut-glands, which, besides their

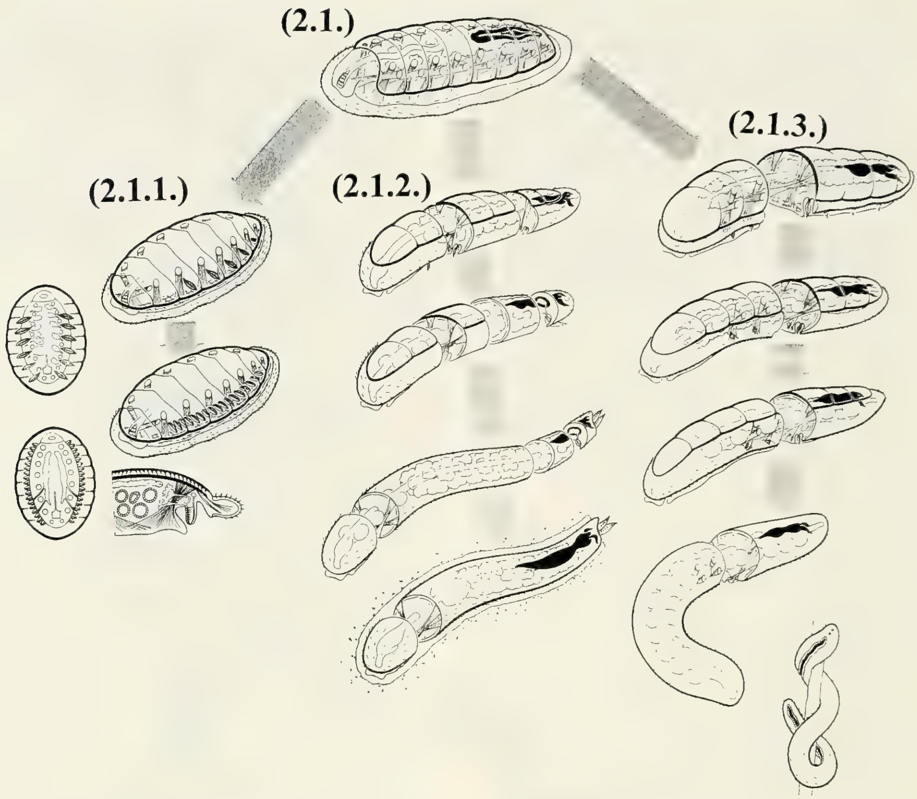

Figure 3. Evolutionary transformation of chiton-like predecessor into Placophora, Caudofoveata and Ventroplicata.
Figura 3. Transformación evolutiva del predecesor tipo quitón en Placophora, Caudofoveata y Ventroplicata.

digestive function, served as newly formed fluid filled entities in the frame of the form enforcing structures and as a substantial part of the filling of the inner spaces of the body. The gut pouches were also helpful in holding the gut in its position. As the coelomic space was restrained by the muscle construction and receded to narrower dorsal cavities glandular kidney structures had to develop as extensions of the metanephridia. They collected excretory material from the extra coelomic spaces mainly in the muscle grid. Such an alteration of the metanephridial excretory organs was necessitated by the enlargement of the extracoelomic fluid fillings of the muscular grid. The coelom inevitably lost its function as the sole fluid filling unit of the body. There can be no doubt that the evolutionary transformation of the muscle apparatus and the restructuring of the excretory system were coupled and mutually dependent.

(2.1.) The Polyplacophoran like transitional stage. The model represents an early organisational constellation in molluscan evolution. These forms retained the metameric organisation of muscle system, shell arrangement, gills, and kidneys (Fig. 3).

(2.1.1.) The fully developed Polyplacophoran constructions represent a side

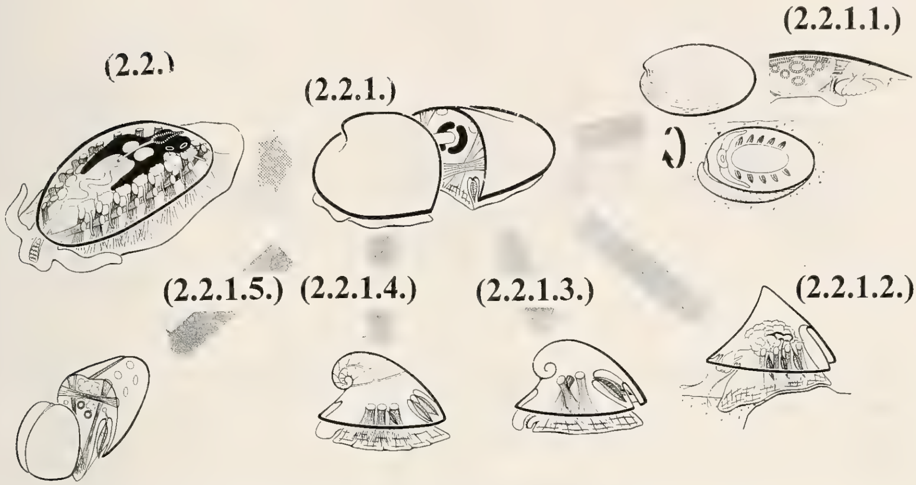

Figure 4. The radiation of conchiferan constructions resulting in diverging organismic types which are capable of occupying different environmental conditions.
Figura 4. Radiación de construcciones conchíferas que resulta en tipos de organismos divergentes capaces de ocupar diferentes condiciones ambientales.

branch of primitive molluscs. Flattening of the shells became more pronounced. The serial shell plates continue to preserve the metameric arrangement of the dorsoventral musculature. In the course of flattening the circulatory and the gill systems were restructured in a way allowing the non-metameric array of the gills and decoupling of internal metamerism and gill-position. This is unique in Polyplacophorans and not representative for the transition to the molluscs with fused shells.

(2.1.2.) Evolution of the Caudofoveatan construction is part of a radiative differentiation of the polyplacophoran organization. This lineage must have started from polyplacophoran forms (EDLINGER, 1989b) which underwent reduction of the shells. Concomitantly with shell reduction the lattice-like muscle foot was only retained in the anterior portion of the worm like body. The gut was also considerably altered; in the rear portion the intestinal canal was surrounded by the midgut-glands, which held the gut in its position. In these burrowing constructions only one posterior pair of gills was retained in the hind part of the body. The resulting worm-like form developed independently of the Ventroplicatan constructions.

(2.1.3.) Evolution of the Ventroplicatan construction is also a branch of Polyplacophoran radiation: loss of shell structures in conjunction with an enlargement of the girdle resulted in the formation of a worm-like body. The foot-complex persisted as a narrow groove running along the ventral side of the whole body length. The groove remains internally tethered by the dorsoventral muscle bundles which are certainly rudiments of the serial shell related retractors. In contrast to the burrowing Caudofoveata the Ventroplicata are capable of climbing in "tree-like" environments. To corroborate the derivation of the worm-like forms from Polyplacophorans it should be kept in mind that some extant Polyplacophorans as *Cryptoplax* show an observable tendency to reduce the shells.

(2.2.) In the evolutionary alley to the Conchiferan constructions (Fig. 4) the Monoplacophorans demarcate a strategic intermediate stage.

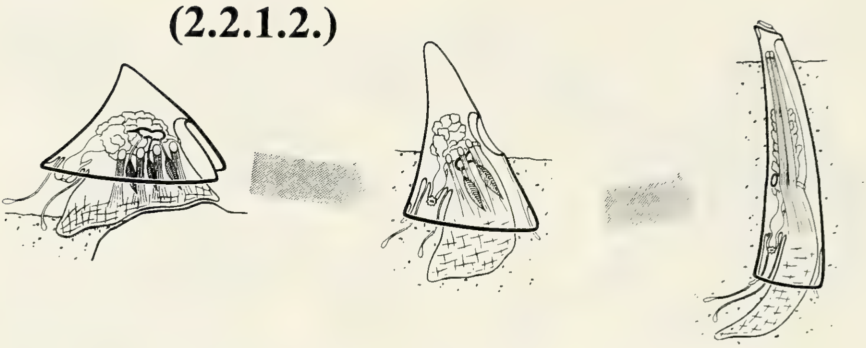

Figure 5. Transformation of monoplacophoran-like ancestors into scaphopods by extreme dorsoventral elongation.
Figura 5. Transformación de ancestros tipo monoplacóforo en escafópodos mediante una elongación dorsoventral extrema.

The unified shell was formed by fusion of the segmental skeletal elements. This process ensued in the deepening of the groove between the cephalopodium and the shell-covered visceral hump. The waist became more pronounced and thereby the cephalopodium was rendered more flexible in respect to the shell. In the Monoplacophora the metameric soft body organization of muscles, gills, nephridia and portions of the coelom is still retained. Metamerism is obviously fading from the rostral portion of the body (GUTMANN, 1974; EDLINGER, 1991a). Noticeable is the concentration of the ancestral structures, coelom, sac bearing nephridia, and gills in the rear part of the body. This situation is indicative of the transition to the other conchiferan constructions which sprang from a radiative divergence of constructions.

(2.2.1.) The fully developed Conchiferan Constructions.

In all conchiferan constructions with fused shells the separation of the two body-portions, the cephalopodium and the dorsal hump, by a waist allows free movement of the foot and the undeformed posture of the visceral sack with the stiff shell frame far from the substrate. The formation of the waist enforced the reduction of the number of gill-pairs in all derived conchiferan constructions.

(2.2.1.1.) Neopilinida.

The Neopilinida are flattened recent Monoplacophoran constructions with clear remnants of metamerism in the arrangement of muscles, nephridia and gills. So they must be early representatives of the transition phase to the Conchiferans. However, clear indications of reduction of metamerism from the anterior portion of the body become evident; the anterior gills are reduced and the muscle bundles fused (GUTMANN, 1974; EDLINGER, 1991a).

(2.2.1.2.) Evolution of Scaphopod constructions.

Scaphopods are derived from a Monoplacophoran stage with a posterior slit in the shell for the expulsion of faeces. A dorsoventral elongation of the construction caused the reduction of the number of muscles and gill pairs and the formation of a tube-like shell. The foot changes its form by a rearrangement of the internal muscle-lattice and becomes a burrowing organ. The posterior slit of the shell became an elongate hole. This hole enabled the animals to ventilate their mantle cavity when they penetrated into the substrate. The water is sucked in from the anterior region and expelled through the posterior hole. The total reduction of the gills is enforced by the narrowing of the mantle cavity when the elongate organisms developed (EDLINGER, 1991b) (Fig. 5).

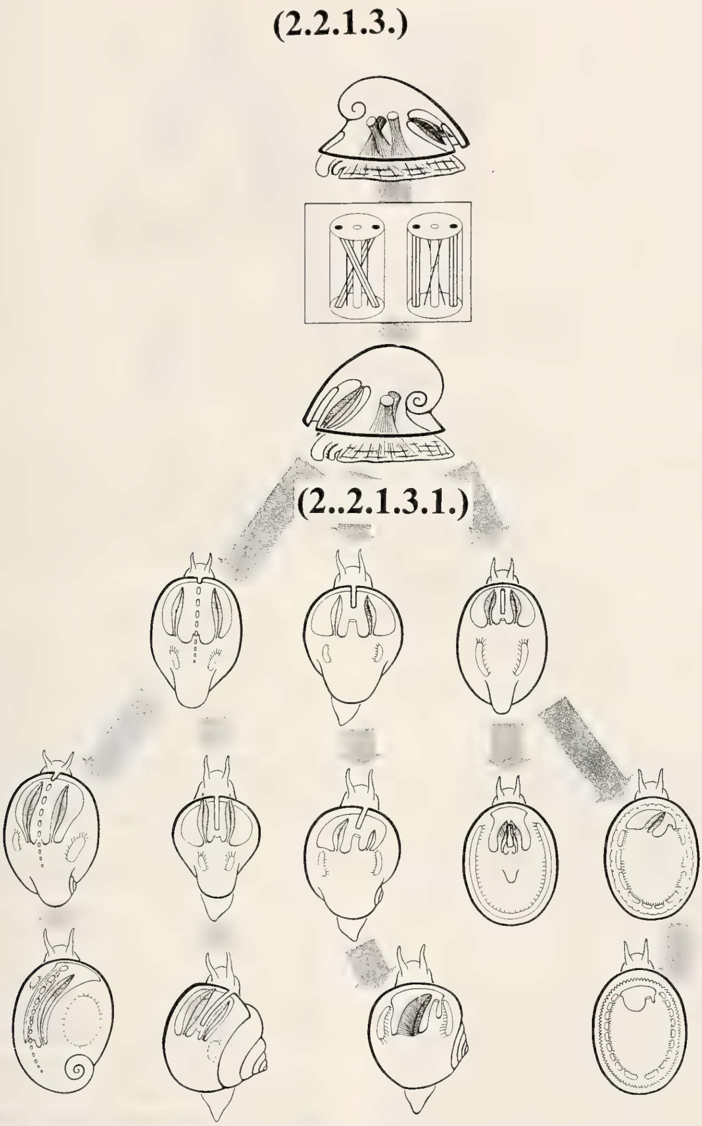

Figure 6. The evolution of the gastropod construction by torsion. Torsion occurs after the formation of a waist between the cephalopodium and the visceral hump and reduction of most of dosoventral muscles.

Figura 6. La evolución de la estructura de un gasterópodo mediante torsión. Ésta ocurre tras la formación de un estrechamiento entre el cefalopodio y el asa visceral, y la reducción de la mayoría de los músculos dorsoventrales.

(2.2.1.3.) Evolution of Gastropods (EDLINGER, 1988a, 1988b, 1989a).

The most significant event of gastropod evolution was the torsion of the visceral hump after a very narrow waist had formed and most of the gill pairs had been reduced. Torsion led to an anterior position of the partially reduced mantle ca-

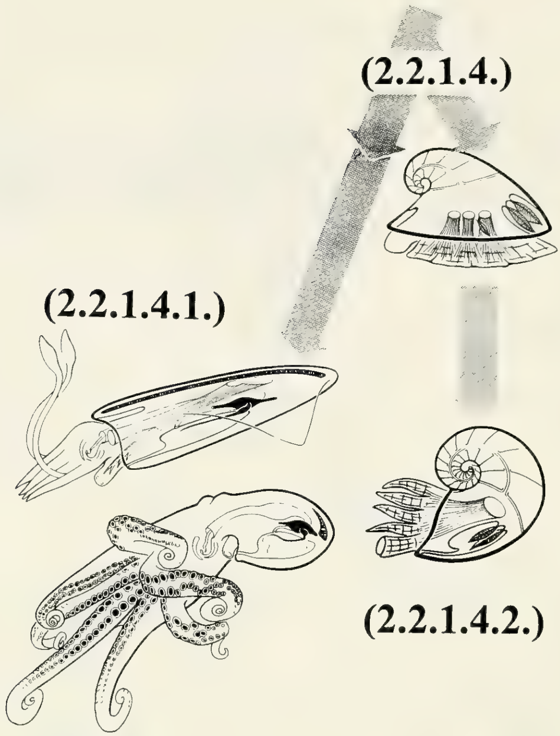

Figure 7. The evolution of cephalopods characterized by the appearance of gas-filled spaces at the top of the shell and by a radical rearrangement of the musculature of the cephalopodium with strong muscular arms and suckers.
Figura 7. Evolución de los cefalópodos, caracterizada por la aparición de cámaras llenas de gas en la parte alta de la concha y una redistribución radical de la musculatura del cefalopodio con fuertes ramas musculares y ventosas.

vity with the remaining gills and the formation of the chiasma of the lateral nerve cords. The precondition for torsion lies in a step by step reduction of dorsoventral muscle bundles of a Monoplacophoran ancestor and by narrowing of the waist between the cephalopodium and the visceral hump. This process is connected with a step by step spiralling up of the shell. The persistence of only one pair of crossing obliquely transversal muscles could cause the torsion. Totally bilaterally organised symmetric Bellerophontacean shells are representative of this process (Fig. 6).

(2.2.1.3.1) Radiation of Gastropod constructions: All gastropod lineages are derived from a Bellerophontacean stage with a bilateral and helical shell, which possessed slits or a series of holes in the posterior part of the shell for the expulsion of faeces. Only one pair of parallel dorsoventral muscles persisted. Asymmetry could arise by the partial or total reduction of one of the dorsoventral muscles and the change of the planispiral shell of Bellerophon-like ancestors to an asymmetric helical form. In most cases the gills became also unequal or one gill was entirely reduced (EDLINGER, 1988a, 1988b, 1989a).

Flattening and secondary reduction of the coil can result in the formation of a cup-like shell. Flattening must cause a change in the muscle arrangement. The dorsoventral muscles and their scares on the inner of the shells were enlarged to form

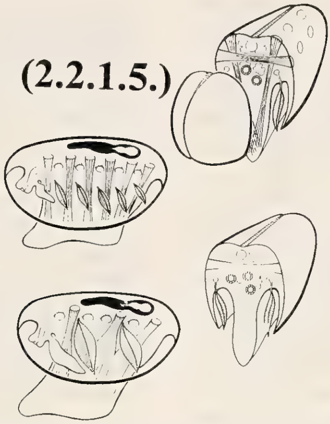

Figure 8. The evolution of bivalves by a rearrangement of the dorsoventral muscles and a division of the shell to a bivalve one.
Figura 8. Evolución de los bivalvos por medio de una redistribución de los músculos dorsoventrales y una división de la concha hacia una concha bivalva.

horseshoe-like insertions. The gills can persist as in *Fissurella*. In this case the retractor muscle will form a homogeneous horse-shoe-like entity. If the gills are also reduced and substituted by secondary gill-like structures the muscles are splitted up into a Monoplacophoran-like situation of *Patella* (EDLINGER, 1988a, 1988b, 1989a; HASZPRUNAR, 1988).

(2.2.1.4.) Evolution of Cephalopod constructions (BONIK, GRASSHOFF, GUTMANN AND KLEIN-RÖDDER, 1977). The development of gas-filled chambers in the apical part of the shell rendered the organisms more buoyant. The foot with its deformability and the adhesive capabilities was altered into a system of muscular arms with suckers which could grasp prey. Retraction of the soft-body into the shell inevitably caused expulsion of a water-current. In the course of evolution improvement of this mechanisms was altered into effective jet propulsion when the hind part of the foot was modified to form a narrow funnel through which the water expelled from the mantle cavity was concentrated to enhance the jet effect. This constructional situation can be observed in all cephalopods (Fig. 7). An early bifurcation or diphyletic development gave rise to the branches of endocochlean and exocochlean Cephalopod construction (2.2.1.4.1, 2.2.1.4.2).

(2.2.1.5.) Evolution of Bivalve Constructions (VOGEL AND GUTMANN, 1980). The origin of Bivalves can be understood as a rearrangement of the dorsoventral muscles in a high chambered Monoplacophoran ancestor. A considerable portion of the dorsoventrally and obliquely arranged muscles in the foot were shifted into a horizontal position connecting not the shell and the foot as in the former stages but the two laterally bent down plates of an evolving bivalved shell. Contraction of the muscles brought the flanks of the shells together in protective behaviour. Most of the vertical (dorsoventral) portions of the musculature retained their original retractile function in respect to the foot but the number of retractors was reduced. Consequently most of the gills disappeared with one pair remaining.

The remaining pair of gills are utilised as filterfeeding devices because lateral cephalic lobes bridged the gap between the mouth and the gills and formed conveyer belts for the transport of food from the gills to the mouth (Fig. 8).

DISCUSSION AND CONCLUSION

It is very obvious that in the perspective of constructional morphology and organismic evolution character-analysis and the establishment of sequences of organismic forms in the sense of homologies are inconclusive and arbitrary. They pose problems but do not provide answers because description of form and character analysis do not lead to constructional insight or an understanding of form determination. Constructional alteration in evolution can not reasonably be derived from genetic or other molecular features (GHISELIN, 1988; WÄGELE, 1994; WÄGELE AND WETZEL, 1994; EDLINGER, 1995). The understanding of organisms as constructions leaves no doubt that the constructional configuration determines evolutionary change of the living machinery and prescribes the sequence of constructional stages and of irreversible steps. There is little freedom for contingency in the order of the "bauplan" configurations and no encouragement for simple description and form comparison. Nothing useful can come from such traditional approaches which are blind to causal aspects and insensitive for explanatory principles.

When organisms are conceived as energy transforming constructions evolution must be ruled by constructional principles and not by subjective "gestalt" properties or subservient molecular mechanisms. As could be shown in the foregoing context strict obeisance of the constructional principles allows the rejection of constructionally impossible or improbable alternatives. From the methodology applied and the mode of reconstruction of the evolutionary transformations just advocated follows that traditional phylogenetic concepts, form sequences, and cladograms based on usual procedures are not considered valid. Therefore, traditional hypotheses are bypassed and left out of consideration when the criteria of the Frankfurt-Theory are applied. If somebody feels the need to adhere to the idea that Plathelminths, non-segmented worms, or Nemerteans might be the precursors of mollusc he or she should present a continuous model with a strict explanation of the intermediate constructional steps.

The genes and other molecular mechanisms which are subservient in relation to the living constructions and their structures have to comply with the constructional requirements and must follow constructional modifications of the machinery in the course of structural reorganisation. Taken as separate features molecular and physiological mechanisms are not useful for the elucidation of constructional change in evolution. Therefore, constructional morphology neglects all traditional suggestions as to the affinity of organismic groups based on form similarities in the sense of homologies and on subservient and constructionally dependent molecular and physiological properties.

It is not possible to give a list of all the published sequences of forms which were figured out to represent what all the authors tried to suggest as stages of mollusk evolution (SCHELTEMA, 1978; GÖTTING, 1980a, 1980b; HAAS, 1981; BANDEL, 1983; LAUTERBACH, 1983a, b; HASZPRUNAR, 1988, 1992a, b). Many contributions were formulated by paleontologists (RUNNEGAR AND POJETA, 1974; RUNNEGAR, POJETA, NOEL, TAYLOR, TAYLOR AND MCCLUNG, 1975; MAREK AND YOCHELSON, 1976; YOCHELSON, FLOWER AND WEBERS, 1973; POJETA JR., 1987) who started from one or the other fossilstructure. Most morphoclines presented since the last century are highly contradictory, however, all of them have in common an access that arbitrarily selects some features of skeletal or soft body structures.

Organisms as constructionally restrained and not deliberately transformable entities are not even expected. In none of the published morphoclines is the directionality of evolutionary transformation elaborated or explained as irreversible. Organisms are misconceived as shaped and freely modifiable pieces of art. Fruitful discussion can only start when alternative models with continuous explanations and well supported transformational polarities are given. In the present situation the discussion of all the morphoclines would require the sacrifi-

cium intellectus. Also in the field of radiation of the phylum Mollusca reconstructions have to be done on the consistent basement of constructional laws and solid criteria of directionality of evolutionary changes. In the recent only the models outlined above meet this conditions. All alternative concepts which will possibly appear must be discussed on the basis of this conditions.

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Mollusc fauna of the medium high mountain ranges of the Hungarian Holocene: a zoogeographical research

Fauna de moluscos de media y alta montaña del Holoceno de Hungría: una investigación zoogeográfica

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ABSTRACT

An attempt is made to complete the zoogeographical studies of the mollusc fauna of the medium-high mountain ranges of the Hungarian Holocene by analysing twenty-eight chronologically and biostratigraphically known faunae. Eighty four species are classified in nine faunal-centres and four biozones (*Vallonia costata*, Clausillidae, *Granaria frumentum* and *Helicigonia faustina – Acicula polita*). A brief discussion is made on the abundance of several species of each faunal-centre. The picture drawn from the fauna agrees with the geographical position and geomorphological conditions of Hungary (Carpatian Basin, Central-Europe)

RESUMEN

Se pretende completar los estudios zoogeográficos de la fauna de moluscos de media y alta montaña del Holoceno de Hungría mediante el análisis de ventiocho faunas conocidas tanto cronológica como estratigráficamente. Ochenta y cuatro especies fueron clasificadas en nueve "centros faunísticos" y cuatro biozonas (*Vallonia costata*, Clausillidae, *Granaria frumentum* and *Heliciqonia faustina – Acicula polita*). Se hace una breve discusión sobre la abundancia de varias especies en cada "centro faunístico". La representación que se obtiene de la fauna coincide con la posición geográfica y las condiciones geomorfológicas de Hungría (planicie de los Cárpatos, Europa central).

KEY WORDS: Molluscs, Zoogeography, Holocene, Hungary.
PALABRAS CLAVE: Moluscos, Zoogeografía, Holoceno, Hungría.

INTRODUCTION

The paleoecological and biostratigraphical studies of the mollusc fauna of the medium-high mountain ranges of the Hungarian Holocene (Fig. 1) has been completed in the last few years. (FÜKÖH, 1991, 1992a, 1992b, 1993a, 1993b). Although during these estudies, zoogeographical examinations were carried out for certain faunae (FÜKÖH, 1983, 1989; BÁBA AND FÜKÖH, 1984), a comprehensive view is lacking. The aim of this paper is to complete the lack of information about this subject.

The analysis of twenty-two chronologically and biostratigraphically known faunae (FÜKÖH, KROLOPP AND SÜMEGI, 1995) is completed in this work (Fig. 2), increasing the number of species previously cited from 81 (Table I) to 84 (Table III).

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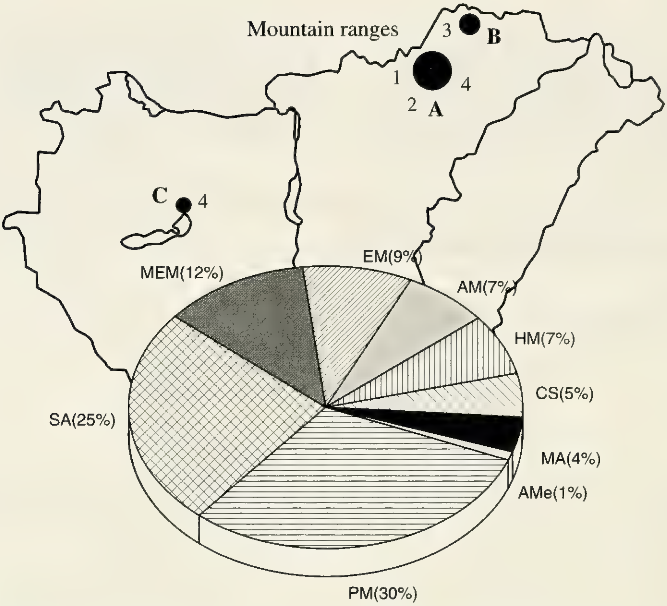

Figure 1. Map showing the position of the localities of the Biozones stratotypes and the zoogeographical distribution of the Holocene mollusc fauna in the Hungarian medium high mountain area. A: Bükk Mts.; B: Aggtelek karst; C: Bakony Mts. Faunal centres, PM: Ponto-mediterranean; SA: Siberian-Asiatic; MEM: Middle-European-Mountain; HM: Holomediterranean; AM: Adriato-Mediterranean; EM: European-Mountain; MA: Middle-Asiatic; CS: Caspi-Sarmatian; AMe: Atlanto-Mediterranean. Biozones, 1: *Vallonia costata* biozone; 2: Clausiliidae biozone; 3: *Granaria frumentum* biozone; 4: *Helicigona faustina – Acicula polita* biozone.

Figura 1. Mapa mostrando la posición de las localidades de los estratotipos de las biozonas y la distribución zoogeográfica de la fauna de moluscos de media y alta montaña del Holoceno de Hungría. A: Montes Bükk; B: karst de Aggtelek; C: Montes Bakony. "Centros faunísticos", PM: ponto-mediterráneo; SA: siberiano asiático; MEM: media montaña europea; HM: holomediterráneo; AM: adriatico-mediterráneo; EM: montaña europea; MA: medio asiático; CS: caspiano-samartiano; AMe: atlanto-mediterráneo. Biozonas, 1: biozona de Vallonia costata; 2: biozona de Clausiliidae; 3: biozona de Granaria frumentum; 4: biozona de Helicigona faustina – Acicula polita.

MATERIAL AND METHODS

The methodology used to carry out the classification presented in this paper is the same employed to situate zoogeographically the species of the Middle-European faunae. These methods can be divided into two main groups as follows:

1. Methods based on recent distribution of the species (KERNEY, CAMERON AND JUNGBLUTH, 1983; FLASAR, 1971; KÖRNIG, 1983; ALEXANDROWITZ, 1983, 1984; FRANK, 1988, 1990, 1992a, 1992b)

2. Derivative method (BÁBA, 1982). This method is based on recent and fossil distribution of the species. This methodology was chosen because, according to the preliminary examinations and calculations, it is more suitable when researching fossil materials.

RESULTS AND CONCLUSSIONS

Table II shows the distribution in number of the 84 mollusc species found in the studied area by faunal-centres and biozones. Figure 3 illustrates the zoogeographical distribution in number of the Holocene and recent mollusc species.

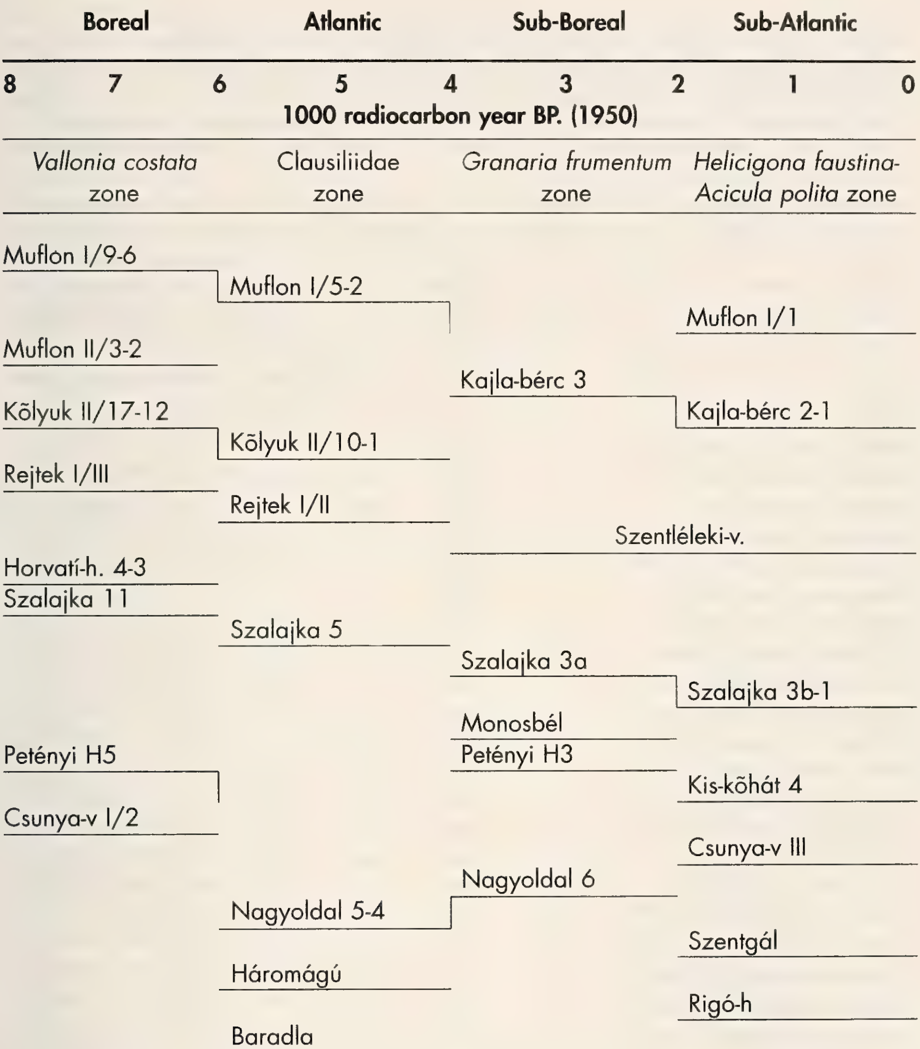

Figure 2. Biostratigraphic identification of significant terrestric Holocene localities of Hungary (twenty-eight chronologically and biostratigraphically known faunae). *Bükk Mts.*: "Muflon"-cave, "Kajla-bérc"-cave, "Kőlyuk II"-cave, "Rejtek I"-cave, "Horvéti"-hole, "Petényi"-cave, "Csunya"-valley I-rock shelter, "Csunya"-valley III-rock shelter, "Háromágu"-cave, "Kajla-bérc"-cave, "Szalajka"-valley-travertine, "Monosbél"-travertine, "Szentléleki"-valley-rock shelter, "Kálmán-rét"-shaft-cave, "Kiskőhát"-shaft-cave. *Aggtelek karst*: "Baradla"-cave, "Nagy-oldal"-shaft-cave. *Bakony Mts.*: Szentgál, Mecsek-hill, "Kő-lik"-cave, "Rigo"-hole. Lines represent the biostratigraphic and chronologic extension and/or connection of localities (shown in Figure 1).

Figura 2. Identificación bioestratigráfica de las localidades terrestres más significantes del Holoceno de Hungría (ventiocho faunas conocidas cronológica y bioestratigráficamente. Montes Bükk: cueva "Muflon", cueva "Kajla-bérc", cueva "Kőlyuk II", cueva "Rejtek I", sima "Horvéti", cueva "Petényi", abrigo rocoso "Csunya"-valley I, abrigo rocoso "Csunya"-valley III, cueva "Háromágu", cueva "Kajla-bérc", valle "Szalajka" travertino, "Monosbél" travertino, valle "Szentléleki" abrigo rocoso, pozo "Kálmán-rét", pozo "Kiskőhát". Karst Aggtelek*: cueva "Baradla", pozo "Nagy-oldal".* Montes Bakony*: Szentgál, Mecsek-hill, cueva "Kő-lik", sima "Rigo". Las líneas representan la extensión y/o conexión bioestratigráfica y cronológica de las localidades (mostradas en la Figura 1).*

Table I: Distribution of 81 molluscs species found the medium-high mountain ranges of the Hungarian Holocene fauna, according to several authors. Authors, 1: Verney, Cameron and Jungbluth; 2: Flasar; 3: Alexandrowicz; 4: Körnig; 5: Frank; 6: Bába. Abbreviations, a: Alpian; adm: Adriatic-Mediterranean; e: European; h: Holarctic; hm: Holomediterranean; k: Carpatian; ksz: Capian-Sarmatian; m: middle; ma: Middle-Asiatic; med: Mediterranean; merid: meridional; p: Palearctic; po: Pontomediterranean; s, n, o, w, the four cardinal points; sza: Siberian-Asiatic; ws: West-Sibiric; sz: Siberian.

Tabla I. Distribución de 81 especies de moluscos encontradas en media y alta montaña de la fauna del Holoceno de Hungría, de acuerdo con distintos autores. Autores, 1: Verney, Cameron and Jungbluth; 2: Flasar; 3: Alexandrowicz; 4: Körnig; 5: Frank; 6: Bába. Abreviaturas, a: alpino; adm: adriatico-mediterráneo; e: europeo; h: holártico; hm: holomediterráneo; k: carpatiano; ksz: capiano-samartiano; m: medio; ma: medioasiático; med: mediterráneo; merid: meridional; p: paleártico; po: pontomediterráneo; s, n, o, w: los cuatro puntos cardinales; sza: siberiano-asíatico; ws: sibírico oeste; sz: siberiano.

Species	**1**	**2**	**3**	**4**	**5**	**6**
Achantinula aculeata (O. F. Müller, 1774)	wp					wsz
Acicula polita (Hartmann, 1840)	e-a	me	me	me	me-a	po
Aegopinella minor (Stabile, 1864)	some	me-se		soe	some	po
Aegopinella pura (Alder, 1830)	e	e		e	e	wsz
Bradybaena fruticum (O. F. Müller, 1774)	moe-a			e	e-a	osz
Bulgarica vetusta (Rossm(ssler, 1836)	soe					po
Carychium minimum (O. F. Müller, 1774)	e-sz	e-sz		e	e-sz	osz
Carychium tridentatum (Risso, 1826)	e	se		e	e	hm
Cecilioides acicula (O. F. Müller, 1774)	med-we				wme	
Cepea vindobonensis (Férussac, 1821)	soe		soe	soe		ksz
Chondrina clienta (Westwrlund, 1883)	soe-a			soe-a	oe-a	po
Chondrula tridens (O. F. Müller, 1774)	msoe	pm			msoe	hm
Clausilia cruciata (Studer, 1820)	ne-a		ba	b-a	moe-a	e
Clausilia dubia Draparnaud, 1805	me	me	me	me	me	po
Clausilia pumila C. Pfeiffer, 1828	moe	me	oe	ome	moe	po
Cochlicopa lubrica (O. F. Müller, 1774)	h	h	ws	h	h	h
Cochlicopa lubricella (Porro, 1837)	h	h		h	h	ma
Cochlodina cerata (Rossm(ssler, 1836)	k			wk		me
Cochlodina laminata (Montagu, 1803)	e	e	ws	e	e	me
Cochlodina orthostoma (Menke, 1830)	moe			oe		me
Columella edentula (Draparnaud, 1801)	h	h			h	o-sz
Daudebardia brevipes (Draparnaud, 1805)	mse				mse	po
Daudebardia helenae Füköh, 1985						me
Daudebardia rufa (Draparnaud, 1805)	mse			med-me	sme	po
Discus perspectivus (Mühlfeld, 1816)	a-ok			a-ok	a-ok	po
Discus rotundatus (O. F. Müller, 1774)	wme	wsm	ws		wme	adm
Discus ruderatus (Férussac, 1821)	p	p		p	p	o-sz
Ena montana (Draparnaud, 1801)	me-k-a	me		me	me-k	e
Ena obscura (O. F. Müller, 1774)	e			e	e	hm
Euconulus fulvus (O. F. Müller, 1774)	h	h		h	h	h
Euomphalia strigella (Draparnaud, 1801)	me	ome		ome	ome	ksz
Granaria frumentum (Draparnaud, 1801)	med			merid	moe	po
Helicella obvia (Menke, 1828)	soe				smoe	
Helicigona faustina (Rossm(ssler, 1838)				k		me
Helicodonta obvoluta (O. F. Müller, 1774)	me	merid		merid	sme	adm

Table I. (Continuation).
Tabla I. (Continuación).

Species	1	2	3	4	5	6
Helicopsis striata (O. F. Müller, 1774)	wmoe				e	
Helix pomatia Linné, 1758	smoe	soe	me	soe	msoe	po
Isognomostoma isognomostoma (Schröter, 1784)	a-k	me	a-k	a-k	a-k	me
Laciniaria biplicata (Montagu, 1803)		me-b		some		po
Laciniaria plicata (Draparnaud, 1801)	moe		me	me	moe	po
Macrogastra latestriata (A. Schmidt, 1857)	k					
Macrogastra plicatula (Draparnaud, 1801)	me	e		e	e	po
Macrogastra ventricosa (Draparnaud, 1801)	me	e	me	e	e	po
Monacha cartusiana (O. F. Müller, 1774)						po
Nesovitrea hammonis (Ström, 1765)	p	p			h	o-sz
Orcula doliolum (Bruguiére, 1792)	soe		me	merid	soe	ma
Orcula dolium (Draparnaud, 1801)	a-k			a-wk	a-k	po
Oxychilus depressus (Sterki, 1880)	a-k	me		a-k		po
Oxychilus draparnaudi (Beck, 1837*)*	med-we				we	
Oxychilus glaber (Rossm(ssler, 1838)	sme	smoe		soe	a-se	po
Oxychilus inopinatus (Ulicny, 1887)	k					
Oxychilus orientalis (Clessin, 1887)	k			k		me
Perforatella incarnata (O. F. Müller, 1774)	msoe	mwe		me	msoe	po
Perforatella vicina (Rossm(ssler, 1842)						e
Punctum pygmaeum (Draparnaud, 1801)	h	p		p	h	h
Pupilla muscorum (Linné, 1758)	h				h	o-sz
Pupilla triplicata (Studer, 1820)	oe-a				e-a	adm
Pyramidula rupestris (Draparnaud, 1801)	we-m		oe	m-a	m-a	ma
Ruthenica filograna (Rossm(ssler, 1836)	oe		oe	moe	moe	me
Semilimax kotulai (Westerlund, 1871)	a-k	a-k		a-k		
Semilimax semilimax (Férussac, 1802*)*	a-me				a-me	
Trichia unidentata (Draparnaud, 1805)	a-k	oa-wk	oa-wk		oa-k	me
Trichia hispida (Linné, 1785)	e				e	
Truncatellina claustralis (Gredler, 1856)	m-sa			m	m	hm
Truncatellina cylindrica (Ferrussac, 1807)	se	se		se	se	hm
Vallonia costata (O. F. Müller, 1774)	h	h	h	h	h	h
Vallonia pulchella (O. F. Müller, 1774)	h	h	h	h	h	h
Vallonia enniensis (Gredler, 1856)	mse	me				
Vertigo alpestris Alder, 1838	na	p				o-sz
Vertigo angustior Jeffreys, 1830	e	e				ksz
Vertigo parcedentata (A. Braun, 1847)						sza
Vertigo antivertigo (Draparnaud, 1801)	p					ksz
Vertigo pusilla (O. F. Müller, 1774)	e	e			e-was	hm
Vertigo pygmaea (Draparnaud, 1801)	h	h			h	wsz
Vertigo substriata (Jeffreys, 1833)	a				a-e	
Vitrea contracta (Westwrlund, 1871)	p					hm
Vitrea crystallina (O. F. Müller, 1774)	e	e	ws	e	e	adm
Vitrea diaphana (Studer, 1820)	a-k			a-merid	a-me	po
Vitrina pellucida (O. F. Müller, 1774)	h	p		p	p	h
Zebrina detrita (O. F. Müller, 1774)	soe					po
Zonitoides nitidus (O. F. Müller, 1774)	h				h	

Table II. Distribution in number of 84 mollusc species in the Hungarian Holocene fauna of the medium-high mountain ranges by Faunal-centres and Biozones. Abbreviations, 1: *Vallonia costata* biozone; 2: Clausiliidae biozone; 3: *Granaria frumentum* biozone; 4: *Helicigona faustina – Acicula polita* biozone.
Tabla II. Distribución en número de las 84 especies de moluscos de la fauna del Holoceno de Hungría en media y alta montaña agrupadas por "centros faunísticos" y biozonas. Abreviaturas, 1: biozona de Vallonia costata*; 2: biozona de Clausiliidae; 3: biozona de* Granaria frumentum*; 4: biozona de* Helicigona faustina – Acicula polita.

		BIOZONES			
FAUNAL-CENTRES	**No. of species**	**1**	**2**	**3**	**4**
Siberian-Asiatic	21	15	19	16	16
Middle-Asiatic	3	3	2	2	2
Caspi-Sarmatian	5	3	4	2	3
Pontomediterranean	25	18	19	18	22
Adriato-Mediterranean	5	5	4	4	5
Atlanto-Mediterranean	1	0	1	0	0
Holomediterranean	6	6	5	5	5
European -Mountain	7	4	3	2	4
Middle-Eur. -Mountain	11	8	6	6	9
TOTAL	84	62	63	55	66

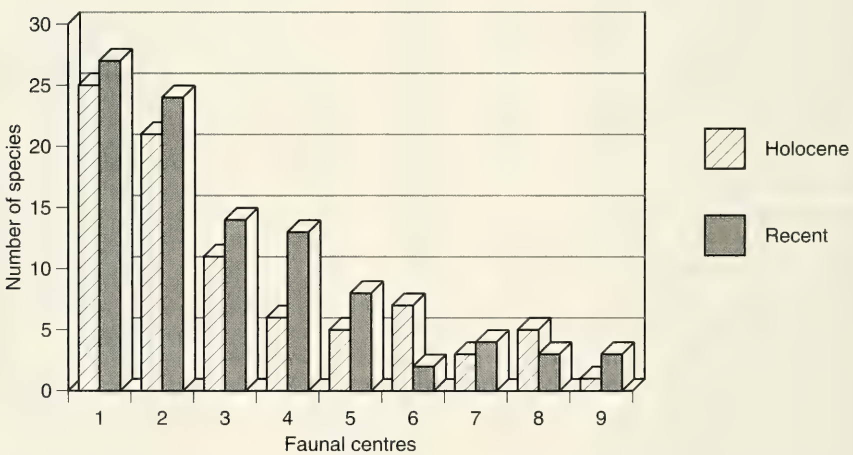

Figure 3. Zoogeographical distribution in number of the mollusc fauna of the Hungarian medium high mountain ranges considering Holocene and Recent species separately. 1: Pontomediterranean; 2: Siberian-Asiatic; 3: Middle-European-Mountain; 4: Holomediterranean; 5: Adriato-Mediterranean; 6: European-Mountain; 7: Middle-Asiatic; 8: Caspi-Sarmatian; 9: Atlanto-Mediterranean.
Figura 2. Distribución zoogeográfica en número de la fauna de moluscos de media y alta montaña de Hungría, considerando tanto las especies del Holoceno como las recientes. 1: pontomediterráneo; 2: siberiano asiático; 3: media montaña europea; 4: holomediterráneo; 5: adriático mediterráneo; 6: montaña europeo; 7: medio asiático; 8: caspiano-samartiano; 9: atlanto-mediterráneo.

Table III. Zoogeographical distribution of the Hungarian Holocene species by faunal-centres. (*) Molluscan species not cited in Table I.
Tabla III. Distribución zoogeográfica de las especies del Holoceno de Hungría por "centros faunísticos". (*) Especies de moluscos no citadas en la Tabla I.

1. Siberian-Asiatic faunal-centres		**21species**
Achantinula aculeata	*Euconulus fulvus*	*Vallonia pulchella*
Aegopinella pura	*Limax maximus* Linné, 1758 (*)	*Vertigo alpestris*
Bradybaena fruticum	*Nesovitrea hammonis*	*Vertigo parcedentata*
Carychium minimum	*Punctum pygmaeum*	*Vertigo pusilla*
Cochlicopa lubrica	*Pupilla muscorum*	*Vertigo pygmaea*
Columella edentula	*Vallonia costata*	*Vitrina pellucida*
Discus ruderatus	*Vallonia enniensis*	*Zonitoides nitidus*
2. Middle-Asiatic faunal centres		**3 species**
Cochlicopa lubricella	*Orcula doliolum*	*Pyramidula rupestris*
3. Caspian-Sarmatian faunal-centres		**5 species**
Cepaea vindobonensis	*Semilimax kotulai*	*Vertigo antivertigo*
Euomphalia strigella	*Vertigo angustior*	
4. Ponto-Mediterranean faunal-centres		**25 species**
Acicula polita	*Granaria frumentum*	*Macrogastra ventricosa*
Aegopinella minor	*Helix pomatia*	*Monacha cartusiana*
Bulgarica vetusta	*Helicella obvia*	*Orcula dolium*
Chondrina clienta	*Zebrina detrita*	*Oxychilus depressus*
Clausilia dubia	*Helicopsis striata*	*Oxychilus glaber*
Clausilia pumila	*Laciniaria plicata*	*Perforatella incarnata*
Daudebardia brevipes	*Laciniaria biplicata*	*Vitrea diaphana*
Daudebardia rufa	*Macrogastra plicatula*	*Vitrea subrimata* (Reinhardt, 1871)(*)
Discus perspectivus		
5. Adriatic-Mediterranean faunal-centres		**5 species**
Cecilioides acicula	*Helicodonta obvoluta*	*Vitrea crystallina*
Discus rotundatus	*Pupilla triplicata*	
6. Atlantic-Mediterranean faunal-centres		**1 species**
Semilimax semilimax		
7. Holomediterranean faunal-centres		**6 species**
Carychium tridentatum	*Ena obscura*	*Truncatellina cylindrica*
Chondrula tridens	*Truncatellina claustralis*	*Vitrea contracta*
8. European-Mountain faunal-centres		**7 species**
Clausilia cruciata	*Oxychilus inopinatus*	*Trichia hispida*
Ena montana	*Perforatella vicina*	*Vertigo substriata*
Macrogastra latestriata		
9. Middle-European-Mountain faunal-centres		**11 species**
Cochlodina orthostoma	*Helicigona faustina*	*Oxychilus draparnaudi*
Cochlodina cerata	*Trichia unidentata*	*Oxychilus orientalis*
Cochlodina laminata	*Isognomostoma isognomostoma*	*Ruthenica filograna*
Daudebardia helenae	*Laciniaria turgida* (Rossmassler, 1836) (*)	

The zoogeographical distribution of species by Faunal-centres is summarised in Table III.

The formation of the characteristic zoogeographical conditions of the recent fauna began after the last cold period of the Pleistocene. This can be stated on the basis of the relative abundance analyses of the faunae (84 species) situated in nine faunal-centres (Tables II and III). Primarily, the abundance of Subatlantic species has increased during the last ten thousand years. Ponto-Mediterranean species are the most important and can be observed almost in all every biostratigraphical zones (*Vallonia costata* biozone 18; *Clausiliidae* biozone 19; *Granaria frumentum* biozone 18; *Helecigona faustina-Acicula polita* biozone 22). Species of the Siberian-Asiatic faunal-centre follow them in importance (*Vallonia costata* biozone 15; *Clausiliidae* biozone 19; *Granaria frumentum* biozone 16; *Helicigona faustina-Acicula polita* biozone 16). The Middle-European-Mountain faunal-centres are located in third place considering the relative abundance of the species (*Vallonia costata* biozone 8; *Clausiliidae* biozone 6; *Granaria frumentum* biozone 6; *Helicigona faustina-Acicula polita* biozone 9).

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Aestivation responses of three populations of the giant African snail, *Achatina achatina* Linne (Gastropoda: Achatinidae)

Respuestas a la estivación de tres poblaciones del caracol gigante africano *Achatina achatina* Linne (Gastropoda: Achatinidae)

Joseph R. COBBINAH*

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ABSTRACT

The rates of aestivation and emergence from aestivation of three experimental populations of the giant African snails *Achatina achatina* (Linne, 1758) were compared. The snails were from three origins: Donyina in the Ashanti Region, Nkasem in the Brong Ahafo Region and Apedwa in the Eastern Region of Ghana. The shortest aestivation period (4 weeks) was recorded for the Apedwa snails while the longest period (16 weeks) was recorded for the Donyina population. Data for pre-aestivation and post-aestivation growth rates show a decreasing order: Apedwa > Nkasem > Donyina. The mean growth rates eight weeks before aestivation were 3.6 g, 14.3 g and 19.2 g for the Donyina, Nkasem and Apedwa snails respectively and differed significantly ($P = 0.001$). The variability in growth rates and duration of aestivation reflects the optimal sizes of the natural population of the three groups.

RESUMEN

Se comparan las tasas de estivación y de abandono de la misma de tres poblaciones experimentales del caracol gigante africano *Achatina achatina* (Linné, 1758). Los caracoles eran de tres localidades diferentes: Donyina, en la región de Ashanti; Nkasem, en la región de Brong Ahafo, y Apedwa, al Este de Ghana. El periodo de estivación más corto (4 semanas) se registró en la población de Apedwa, mientras que el periodo más largo (16 semanas) se registró en la población de Donyina. Los datos de las tasas de crecimiento en la pre-estivación y la post-estivación muestran un orden decreciente: Apedwa > Nkasem > Donyina. Las tasas medias de crecimiento ocho semanas antes de la estivación eran 3,6 g, 14,3 g y 19,2 g para los caracoles de Donyina, Nkasem y Apedwa, respectivamente, y diferían significativamente ($P = 0{,}001$). La variabilidad en las tasas de crecimiento y la duración de la estivación reflejan los tamaños óptimos de las poblaciones naturales de los tres grupos.

Key words: The giant African Snail, *Achatina achatina*, aestivation, Ecotypes.
Palabras clave: Caracol gigante africano, *Achatina achatina*, estivación, ecotipos.

INTRODUCTION

Achatina achatina (Linne, 1758) is found in the closed forest area in Ghana. It shows an annual activity which is maximal in the rainy season and minimal in the dry season. The snail burrows into the upper 10-15 cm

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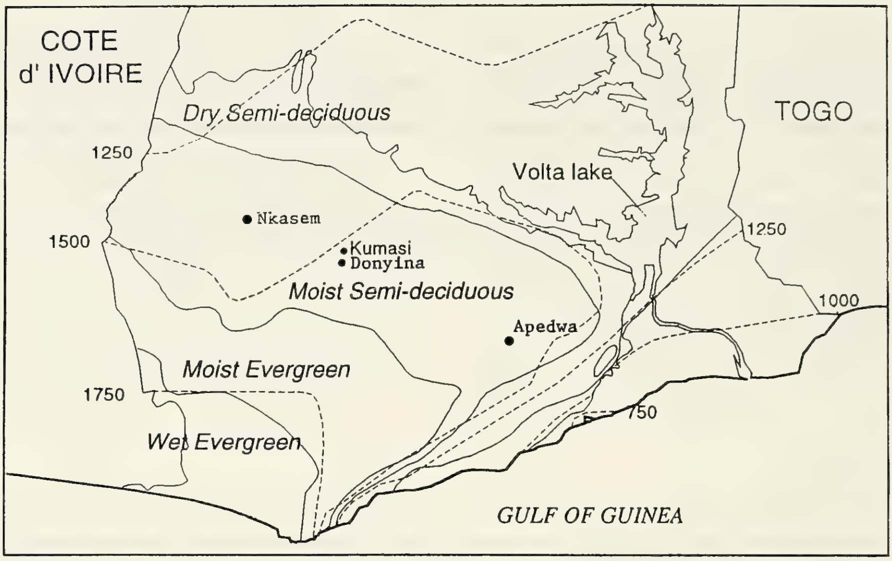

Figure 1. Map of the closed forest area of Ghana showing the trial site (Kumasi) and the origins (Donyina, Nkasem and Apedwa) of the snails used in trials.
Figura 1. Mapa del área de bosque cerrado en Ghana mostrando el lugar del experimento (Kumasi) y los orígenes de los caracoles usados en el mismo (Donyina, Nkasem y Apedwa).

of soil during the dry season and remains dormant for a period ranging from three to five months (COBBINAH, 1993). This state of dormancy during the dry season is referred to as aestivation. Circannual rythms are known to be induced by such factors as light, temperature, humidity and soil water deficit (OWEN, 1966). In the period leading to the onset of aestivation, there is a progressive decline in the snail's metabolism. BARATOU (1988) asserts that in order to maintain an equilibrium between water in its tissue and the relative humidity of the immediate environment, snails allow themselves to dehydrate during this period. For *Achachatina marginata* dehydration leads to the loss of about 42% liveweight of the non-shell tissues (STIEVENART, 1994). Later, a mucous layer is secreted to cover the shell opening; the fully formed mucous layer is impervious to both gases and water (HODASI, 1982). Snails go into a state of dormancy whenever conditions are too dry for their liking. Whilst this behaviour is most common in the dry seasons, COBBINAH (1993) reported that even dry spells during the wet seasons may induce aestivation in *A. achatina*.

This is, however, in contrast to the observation of HODASI (1982) that extensive and persistent dry conditions are necessary to induce aestivation, and that aestivation normally does not occur during the dry spells in the rainy season. Extremes of temperature and starvation is also reported to induce aestivation (KONDO, 1964).

HODASI (1982) suggested that not every individual in the population aestivates during the dry season. Accordingly in certain localities within the distribution range of *A. achatina* in Ghana, fresh snails can be obtained throughout the dry season. Here the results of studies undertaken to determine the variability in aestivation responses of populations from three distinct enclaves of *A. achatina* in Ghana is reported.

MATERIALS AND METHODS

Sources of Snails: The snails for the study were obtained from (a) Donyina in the Ashanti Region, (b) Nkasem in the Brong Ahafo Region and (c) Apedwa in the Eastern Region. Donyina is 20 km from our test site on the campus of the University of Science and Technology, Kumasi, Ghana. Nkasem to the north west and Apedwa to the south east of Donyina are 109 and 198 km respectively from our test site. Figure 1 shows the origin of the three populations together with approximate isohyets. Donyina (6° 45′ N and 2°25′ W), Nkasem (6° 15′ N and 2° 20′ W) and Apedwa (6° 46′ N and 1° 25′ E) all fall within the rainfall regime 1250 mm-1750 mm typical of the moist semi-deciduous forest type. Seasonal rainfall at the three origins is influenced by meteorological Equator (ME). Two weather systems are associated with the ME, the Intertropical Front and the Intertropical Convergence Zone which cause short heavy rain storms and abundant continuous rain respectively and result in bimodal annual rainfall pattern with major rains falling between April-June and minor period of rains between September and October separated by two months of less frequent rains (LEROUX, 1988). The mean annual rainfall for the three locations are Donyina (1403 mm), Nkasem (1395 mm) and Apedwa (1561 mm). The main dry season falls between December and March. The soils at the three areas are of the forest ochrosols type. While all three areas fall within one forest vegetation type, different levels of logging and agricultural practices have resulted in varying rates of deforestation. The Donyina site has completely been converted into farmland over the years. The Apedwa site falls within the mountainous Atewa range protection forest reserve where timber exploitation is prohibited. However, pockets of illegal farms are not uncommon. The Nkesem site is an off reserve area with fairly dense vegetation interspersed with farmlands.

Growth Rates: The snails were conditioned in our research plot for four weeks on a diet consisting of pawpaw (*Carica papaya*) leaves and fruits, cocoyam (*Xanthosoma mofafa*) leaves, and leaves of the fameflower plant (*Talinum triangulare*). Individuals that showed signs of inactivity during this period were not used for the trials. Twenty snails of each group (ecotype) were placed in wooden boxes measuring 0.6 x 0.6 x 0.35 m, filled to a depth of 20 cm with sieved sterile silty sandy soil obtained from an abandoned rubbish dump. The snails in the boxes were offered excess amounts of food but left over foods were removed daily and soils overturned weekly. Because of high survival rates of *A. achatina* (COBBINAH AND OSEI-NKRUMAH, 1988) and insignificant changes in shell size over short periods of time, growth rates were measured by changes in live weights of snails. Each treatment was replicated three times, with data recorded for eight weeks prior to onset of aestivation and eight weeks after emergence from aestivation.

Aestivation patterns of the three populations: The aestivation patterns of individual snails used in the growth studies described above were monitored. Snails were considered as having aestivated when they covered the shell opening with a white mucous layer. Snails were recorded as emerged from aestivation when they discarded the epiphragm and resumed feeding.

A second trial was conducted to determine the effects of increased humidity. Each group of snails was divided into two lots. Twenty snails from one lot were placed in a 0.6 x 0.6 x 0.3 m wooden box as described above. A second set of 20 snails of the same ecotype was placed in another box with humidity slightly increased by making a platform about 15 cm above the soil level and placing a moistened fibre bag on the platform. The bag was kept moist for two weeks before onset of aestivation and throughout the aestivation period. Similar sets were set up for the other ecotypes and each treatment was replicated three times.

All snails used in the studies were labelled (paint marked) to enable observation of individual activities daily. Aestivation responses (time of onset and

Table I. Growth rates of three populations of *Achatina achatina* eight weeks before and after aestivation period.
Tabla I. Tasas de crecimiento de las tres poblaciones de Achatina achatina *ocho semanas antes y después del periodo de estivación.*

Ecotype	Mean initial weight (g) ± s.e.	Mean weight gained in 8 weeks before aestivation ± s.e.	Mean weight gained in 8 weeks after aestivation ± s.e.
Donyina	46.6+1.25	3.60+0.58^{a}	10.83 + 0.17^{a}
Nkasem	49.7+0.95	14.27+0.81^{b}	12.47+ 0.35^{a}
Apedwa	55 + 1.5	19.20+1.37^{c}	19.58 + 2.87^{b}

Means within a row followed by the same letter are not significantly different (P= 0.05).

emergence from aestivation) were recorded for all snails. The time required for 50% of each group to aestivate (TEs_{50}) or emerge from aestivation (TEm_{50}) was estimated for the various treatments and populations.

RESULTS AND DISCUSSION

Growth rates of the three populations: The pre-aestivation growth rates for the Nkasem and Apedwa snails were four and five times more than that recorded for the Donyina snails. The mean growth rates 8 weeks before aestivation ranged from 3.6 g for Donyina to 19.2 g for Apedwa (Table I).

Analyses of the data (ANOVA) in Table I indicate that the growth rates among the three populations differed significantly for the pre-aestivation ($F = 83.94$; $df = 2, 6$; $P< 0.001$) and post-aestivation ($F = 7.73$, df 2, 6; $P< 0.02$) periods. However, Fisher's Multiple Range Test (LSD) did not show significant difference in the post-aestivation growth rates between the Donyina and Nkasem snails. The very low growth rates recorded for the Donyina group 8 weeks before aestivation suggest that, perhaps, aestivation in this group is preceded by significantly longer period of inactivity. Both the pre and post aestivation growth rates of the three populations indicate that the Apedwa group might be the most desirable group for commercial snail farming.

Aestivation Patterns of the three Populations: Figure 2A shows the aestivation pattern of the entire snail population. It took 10 weeks for all the snails in the test to aestivate. Three peaks are found in the second, sixth and tenth week. The three peaks show the heterogeneity in the response of the entire population to factors inducing aestivation.

Figure 2B shows the aestivation pattern of the Donyina ecotype. Aestivation commenced on 29 October 1993 and peaked on 6th November, 1993, one week after the beginning of aestivation. The entire Donyina group aestivated in 5 weeks. The first observation of aestivation for the Nkasem (Fig. 2C) and Apedwa (Fig. 2D) groups was recorded on 6th November, 1993 but peak aestivation for these two groups was recorded on 4th December, 1993 and 28th December, 1993, respectively. Aestivation for these two groups spanned a period of 8 and 9 weeks. Time taken for 50% of each population to aestivate (TEs_{50}) were 8, 28 and 52 days for Donyina, Nkasem and Apedwa snails respectively.

The relatively longer periods required for the Nkasem and Apedwa populations to complete aestivation is a reflection of the variability within these two populations. The peaks observed in Figures 2B-D corresponded to the peaks in Figure 2A and suggest that the heterogeneity in the aestivation pattern of *A. achatina* observed in our study was due mainly to the varia-

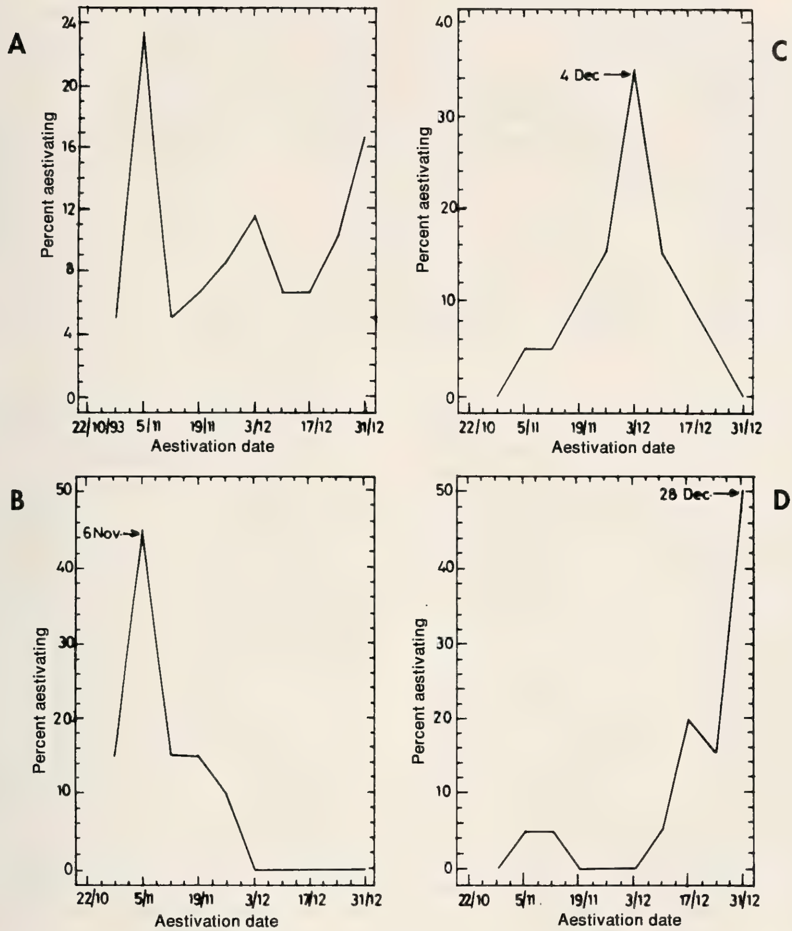

Figure 2. Aestivation patterns. A: entire experimental population; B: Donyina population; C: Nkasem population; D: Apedwa population.
Figura 2. Patrones de estivación. A: toda la población experimental; B: población de Donyina; C: población de Nkasem; D: población de Apedwa.

tion in the responses of the three groups to the factors inducing aestivation.

The emergence period for the entire population covered a period of 7 weeks from the end of January to mid-March, 1994. Again three peaks were evident (Fig. 3A). These were in the third, fifth and seventh week and corresponded to peak emergence periods for the Apedwa (Fig. 3D), Nkasem (Fig. 3C) and Donyina (Fig. 3B) respectively. The first snail to emerge from aestivation was from the Apedwa group on 31 January 1994 (Fig. 3D). By mid-February 60% of this group had emerged from aestivation. On the other hand, not a single snail from the Donyina group had emerged by mid-February, three and half months after initiation of aestivation (Fig. 3B). Twenty percent of the Nkasem group had resumed normal metabolic activities by mid-February (Fig. 3C). Peak emergence in the Donyina group was recorded during the first week in March. Time taken for 50% of population to emerge from aestivation (TEm_{50}) following the outset of emergence were 9,

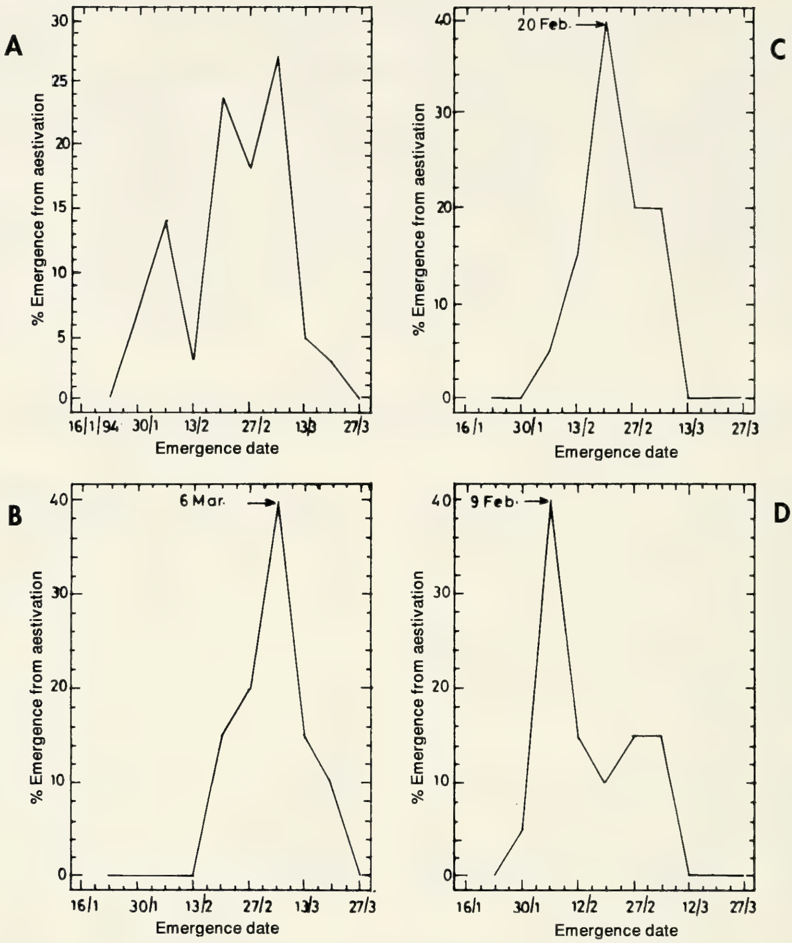

Figure 3. Emergence patterns. A: entire experimental population; B: Donyina population; C: Nkasem population; D: Apedwa population.

Figure 3. Patrones de salida de la estivación. A: toda la población experimental; B: población de Donyina; C: población de Nkasem; D: población de Apedwa.

20 and 33 days for Apedwa, Nkasem and Donyina groups respectively.

Humidity is considered a major factor affecting aestivation behaviour of *A achatina*. COBBINAH (1993) reported that when the relative humidity falls during the dry season *A. achatina* becomes inactive, seals itself in its shell with a white calcareous layer and aestivates in order to prevent loss of water from the body. In this study the enhanced humidity (3% above the ambient condition) attained in the boxes with moistened fibre bags did not influence the overall aestivation pattern of any of the three groups (see Table II).

Elmslie (pers. comm.) asserts that aestivation/hibernation may be influenced by a programmable regulation, resettable by environmental experience like circadian rhythm, but transmitted to offspring in the case of parents that have changed environment in a partially reset state. It is possible that the enhanced humidity in these boxes was not adequate to destabilise the in-built mechanism which sets in motion physiological

Table II. Aestivation patterns of snails in boxes with or without moistened fibre bags.
Tabla II. Patrones de estivación de los caracoles en cajas con o sin bolsas de fibra humedecidas.

Ecotype	Mean Weekly Dry (68-70% rh)	% Aestivation Moist (68-74% rh)	Mean weekly Dry (57-62% hr)	% Emergence Moist (56-66% rh)
Donyina	22.16	23.91	26.54	25.49
Nkasem	19.42	19.57	15.72	16.52
Apedwa	20 96	23.91	13.97	14.80

All differences are not significant at (P = 0.05).

changes resulting in aestivation during periods of low atmospheric humidity.

Whilst aestivation has adaptive value for the snail (HODASI, 1982; STIEVENART, 1994), for the snail farmer it represents the loss of valuable growing time. The three populations show significant differences in growth rates and duration of aestivation. Shorter aestivation period mean longer feeding period and ultimately larger body sizes.

Based on peak aestivation and emergence periods for the three groups, the estimated duration of the dormant periods were 4, 10 and 16 weeks for the Apedwa, Nkasem and Donyina respectively. Moreover, data on growth rates clearly show a decreasing order Apedwa > Nkasem > Donyina among the three groups during the pre and post aestivation periods. These two factors acting in concert may explain differences in adult sizes of *A. achatina* from various areas of the country. The Apedwa snails are usually twice the size of the Donyina snails (COBBINAH, 1993). The Nkasem snails are often intermediate in size between the two populations.

Although all the three enclaves where the snails originated from are within the moist semi-deciduous forest type and are characterized by similar soil type, there are differences in mean annual rainfall and vegetation cover. Soil water regime are influenced by rainfall gradient and evapotranspiration (VAN ROMPAEY, 1993). Most studies of the soil water regime in West African tropical forest (HUTTEL, 1975; COLLINET, MONTENEY AND POUYAUD, 1984) suggest that seasonal soil water deficits increase with decreasing annual rainfall. Mean annual rainfall is highest at Apedwa (1561 mm) but similar at Donyina (1403 mm) and Nkasem (1359 mm). In the three enclaves the Donyina area is the most degraded due to logging and slash and burn agriculture practices over the years. Unlike Apedwa and Nkasem where snails are mainly gathered from forest reserves and secondary forests outside reserves, the Donyina snails are mainly gathered from low vegetation farmlands. Although Donyina and Nkasem have similar mean annual rainfall, the relatively poor vegetation cover at Donyina would result in higher evapotranspiration and longer duration of seasonal drought. The snails from this area have probably adapted to this relatively long drought period through extension of dormancy period.

All individuals in the three groups aestivated in these studies. Nevertheless, a few individuals among the Apedwa group had shorter periods of aestivation than the four week group average. Further studies are, however, underway to determine whether some individuals or groups normally remain active throughout the dry season, and also to better understand the physiological, environmental and behavioural factors controlling aestivation. If the variability in the aestivation behaviour by the different individuals or groups has a significant genetic component, the resulting information would be of potential use for commercial snail farming.

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Snail communities associated to swampy meadows and sedgy marshy meadows plant communities of the Great Hungarian Plain

Comunidades de moluscos asociadas a comunidades vegetales de praderas pantanosas y junqueras en la Gran Llanura Húngara

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ABSTRACT

Simultaneous phytocoenological, malacological and pedological studies were carried out in six successional plant community types characteristic on the Great Hungarian Plain. Data were analyzed by multivariate statistical methods (PCA). Variation in the abundance of ecological, habitat type and nutritional type species groups was also followed. In the *Succiso-Molinietum* (swampy meadows) and *Agrostio-Caricetum* (sedgy marshy meadows) plant communities, the distribution of constant and differential species is mostly influenced by their range of pH tolerance. Habitat drying and salinization, and various human impacts (draining, cutting and grazing by domestic animals) influence the succession of vegetation. Changes in snail assemblages include altering proportion of living and dead individuals and decreasing diversity (H'), both reflecting habitat drying and salinization. Complementary changes in the abundance of riparian and steppe dweller species groups indicate habitat drying, while swamp dwellers become more numerous as the topsoil becomes muddy due to salt accumulation. Concerning nutritional types, the proportion of omnivores decreases with habitat drying, whereas the frequency of herbivores increases in a complementary manner. The increasing abundance of saprophagous snails reflects biotope eutrophization caused by cutting and grazing.

RESUMEN

Se han desarrollado simultaneamente estudios fitocoenológicos, malacológicos y pedológicos en seis tipos de comunidades vegetales de la Gran Llanura Húngara. Los datos fueron analizados mediante métodos estadísticos multivariantes. También se ha estudiado la variación en los grupos de especies desde el punto de vista ecológico, de su hábitat y tipo nutricional. En las comunidades vegetales *Succiso-Molinietum* (praderas pantanosas) y *Agrostio-Caricetum* (junqueras), la distribución de las llamadas especies constantes y diferenciales está mayoritariamente influenciada por su rango de tolerancia de pH. La desecación del hábitat y su salinización, junto con un conjunto de alteraciones humanas (desecación, segado y ramoneado por animales domésticos) afectan la suceción vegetal. Los cambios en las comunidades de moluscos incluyen la variación en las proporciones de individuos vivos y muertos y una menor diversidad (H'); ambos cambios reflejan la desecación y salinización del hábitat. Cambios complementarios en la abundancia de los grupos de especies ribereñas y de estepa son indicadores de la desecación, mientras que las especies propias de zonas pantanosas se hacen más abundantes según la capa super-

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ficial se vuelve fangosa debido a la acumulación de sal. Por lo que se refiere a los grupos nutricionales, la proporción de omnivoros decrece con la desecación, mientras que la frecuencia de herbivoros crece de manera complementaria. La creciente abundancia de especies saprófagas refleja la eutrofización producida por el segado y ramoneo.

KEY WORDS: Gastropoda, drainage, salinization, species groups, succession, Hungary.
PALABRAS CLAVE: Gastropoda, desecación, salinización, grupos de especies, sucesión, Hungría

INTRODUCTION

Under the semiarid climate characteristic to the Eupannonicum floristic region (which the lowlands of the Carpathian Basin belong to), habitat drying and salinization processes were studied along a successional series spanning from swampy to salt-affected meadows. The *Succiso-Molinietum* association represents the wet meadows on calcareous swampy meadows soils. The physiognomy of its vegetation is determined by tall grasses (*Molinia caerulea, M. arundinacea, Festuca pratensis, Deschampsia caespitosa, Agrostis stolonifera*). Its stands have high species diversity and are rich in protected rare species (*Dactylorrhiza incarnata, Orchis laxiflora palustris, Cruciata pedemontana, Veratrum album, Iris spuria, I. sibirica, ...*). The *Succiso-Molinietum* is in successional relation to the *Agrostio-Caricetum* association; namely, moderate habitat drying and salinization involve its transformation into the latter. The *Agrostio-Caricetum* may occur independently, too. It is characteristic of the solontschak-solonetzic alkaline meadows soils. Depending on the hydro- and haloecological conditions the *Agrostio-Caricetum* forms various vegetation units (eg. subassociations), that well reflect the environmental impacts. These units are extremely diverse in its species composition and their physiognomy. The two associations represent the meadow formation of the Great Hungarian Plain in a significant percentage. As the two associations have evolved under wet conditions, the drought on their habitats causes drastical transformation in their vegetation structure, first of all in their species composition. The changes in the structure show close relationship to the environmental conditions, therefore every distinguished vegetation unit well reflects a stage of the drought induced vegetation transformation processes (phytocoenological indication). A lower proportion of data regards to other plant associations, that are in successional relationships with *Succiso-Molinietum* and *Agrostio-Caricetum*.

The water management works in the 20th century and the more and more arid climate of the last two decads endangered the vegetation of the wet meadows. Their transformation into drier habitats would have harmful consequences for the whole ecosystem, particularly the animal assemblages, that have no enough mobility to change their habitat. The terrestrial snails belong to a little mobile group of animals, they are bound to their habitats more firmly than other ones; therefore the, however well-known, successional and zonational relationships of the vegetation units can be examined on the basis of their snail assemblages, too. If the transformation processes of vegetation and their animal assemblages show paralelism, the changes in the composition of this animal group would have an indicative value for nature conservation.

MATERIALS AND METHODS

In the South-eastern part of the Great Hungarian Plain (Csongrád County) snail assemblages were sampled by the quadrat method. Ten plots 25 x 25 cm size were examined in parallel with phytosociological recording of

each plant subassociation encountered (SOÓ, 1964). A hight proportion of the data regards to two plant communities: *Succiso-Molinietum* and *Agrostio-Caricetum;* only some samples originated other successionally related association. Altogether 30 collection sites were visited in six plant community types, while the number of subassociations studied was 22 (see Figure 3). In each quadrat, a detailed soil analysis was conducted, including measurements of relative percentage soil moisture, total organic matter content, $CaCO_3$ concentration, hygroscopy and pH.

The concepts applied in the coenological characterization are the following: Abundance (A) is the number of individuals of a snail species found in a plant community regarding to one m^2 (A/m^2); Dominance (D) is the ratio of individuals of a species related to the total individuals of every species; Species density (SD) is the average species number of 10 quadrats in a collection site; Frequency (F) is the ratio of a species in relation to the total number of species in a collection site (consist of 10 quadrats); Constancy (K) is the ratio of a species in relation to the number of all species found in all collection sites belonging to the same plant community. When a species was found in all the quadrats, it can be considered as an absolute constant species. D, F and K are expressed as percentages.

Data were analyzed by standardized Principal Components Analysis (PCA, PODANI, 1988). Shannon-diversity (H'), SD and changes in the abundance (A/m^2) of living and dead individuals were followed through examination of the proportions of various species groups. Ecological species groups were defined as follows: S: sciophilous, P: swamp dweller, Ph: photophilous, R: riparian and OA: species of open areas. They were obtained by applying the block cluster method of FEOLI AND ORLÓCZI (1979). A simplified version of LOŽEK'S (1964) typology was used and the following habitat type groups were distinguished: riparian ubiquitous (RU), bush forest dweller (B), hygrophilous swamp dweller (HP) and steppe dweller (ST). Nutritional type groups (O: omnivore, SP: saprophagous, H: herbivore) were differentiated after the system of FRÖMMING (1954). Species and their group assignments are listed in Table I.

RESULTS AND DISCUSSION

Species encountered: Field studies yielded a collection of 3047 living and 3150 dead individuals belonging to 26 species (Table I). The majority of the specimens was found in the *Succiso-Molinietum* (1062 + 1268) and *Agrostio-Caricetum* (1496 + 1445) phytocoenoses, while plant associations 1, 3, 4 and 6 altogether contained 489 + 440 alive and dead individuals, respectively.

Two species new to the southern part of the Great Hungarian Plain were detected: *Malacolimax tenellus* (O. F. Müller, 1774) and *Deroceras sturanyi* (Simroth, 1894).

Characteristic species and their requirements: On the basis of frequencies of occurrence data, the constant, subconstant and accessorial species could be determined for the two plant associations most rich in snails (Table II). Constant and subconstant species reach low levels of dominance in both communities. This is probably due to unfavourable changes in their environment caused by either draining, drying, salinization or grazing. Differential species are *Cochlicopa lubricella* (Porro, 1938) and *Carychium minimum* O. F. Müller, 1774 in the *Succisio-Molinietum* plant association, and *Pupilla muscorum* (L., 1758) in the *Agrostio-Caricetum*. The occurrence of *Truncatellina, Granaria* and *Helicopsis* species in the *Agrostio-Caricetum* association indicates habitat drying. The distribution of constant and differential species is strongly influenced by the width of their pH tolerance range (Figs. 1, 2), as it has been shown earlier (BÁBA AND DOMONKOS, 1992). According to aur data differential species of the *Succisio-Molinietum* association have a narrow pH tolerance range, in contrast with species occurring

Table I. Gastropod species found in the plant communities studied (1: *Caricetum acutiformis-ripariae*; 2: *Succiso-Molinietum*; 3: *Bolboschoenetum maritimae*; 4: *Astero-Agrostietum*; 5: *Agrostio-Caricetum distantis*; 6: *Achilleo-Festucetum pseudovinae*) E: Ecological species groups (S: sciophilous; P: swamp dweller; Ph: photophilous; R: riparian; OA: species of open areas); N: Nutritional type (O: omnivore; SP: saprophagous; H: herbivore); H: Habitat type (RU: riparian ubiquitous; B: bush forest dweller; HP: hygrophilous swamp dweller; ST: steppe dweller).

Tabla I. Especies de gasterópodos encontradas en las comunidades vegetales estudiadas (1: Caricetum acutiformis-ripariae*; 2:* Succiso-Molinietum*; 3:* Bolboschoenetum maritimae*; 4:* Astero-Agrostietum*; 5:* Agrostio-Caricetum distantis*; 6:* Achilleo-Festucetum pseudovinae*) E: Grupos ecológicos de las especies (S: esciófilo; P: de marisma; Ph: fotófilo; R: ribereño; OA: de áreas abiertas); N: Tipo nutricional (O: omnívoro, SP: saprófago, H: herbívoro); H: Tipo de hábitat (RU: ribereño ubiquo; B: zonas arbustivas; HP: marismeño higrófilo; ST: estepa).*

E	N	H		1	2	3	4	5	6
S	SP	R	*Carychium minimum* (O. F. Müller 1774)	17	5				
S	SP	HP	*Carychium tridentatum* (Risso 1826)		8				
OA	H	B	*Cepaea vindobonensis* (Ferussac 1821)		1	2		6	
OA	SP	ST	*Chondrula tridens* (O. F. Müller 1774)		135		1	388	50
R	O	B	*Cochlicopa lubrica* (O. F. Müller 1774)		3			4	
OA	O	ST	*Cochlicopa lubricella* (Porro 1838)	+	184				
R	O	RU	*Deroceras laeve* (O. F. Müller 1774)		1				
R	O	HP	*Deroceras sturanyi* (Simroth 1894)		1				
OA	O	B	*Euconulus fulvus* (O. F. Müller 1774)	4					
OA	H	ST	*Granaria frumentum* (Draparnaud 1801)	+				86	
OA	H	ST	*Helicella obvia* (Menke 1828)						3
OA	SP	ST	*Helicopsis striata* (O. F. Müller 1774)					1	
Ph	H	B	*Helix pomatia* (Linne 1758)					2	
S	O	RU	*Malacolimax tenellus* (O. P. Müller 1774)		1				
P	H	ST	*Monacha carthusiana* (O. F. Müller 1774)	18	99	13	5	195	25
R	H	RU	*Perforatella rubiginosa* (A. Schmidt 1853)		3				
OA	H	ST	*Pupilla muscorum* (Linne 1758)	1	1			329	165
R	O	RU	*Succinea oblonga* (Draparnaud 1801)	8	169	43	6	130	+
P	O	HP	*Succinea elegans* (Risso 1826)	1					
OA	SP	ST	*Trucatellina cylindrica* (Ferrusac 1807)					3	
OA	H	ST	*Vallonia costata* (O. F. Müller 1774)	1				8	6
R	O	P	*Vallonia enniensis* (Gredler 1856)	69	390			244	
R	SP	ST	*Vallonia pulchella* (O. F. Müller 1774)	19	40			55	17
R	SP	RU	*Vertigo antivertigo* (Draparnaud 1801)		1				
R	SP	ST	*Vertigo pygmaea* (Draparnaud 1801)	1	20			44	2
R	O	RU	*Zonitoides nitidus* (O. F. Müller 1774)	12				1	
	Number of Individuals			151	1062	58	12	1496	268
	Number of collection sites			1	11	1	1	15	1
	Number of Species			11	17	3	3	15	7
	Dead Individuals			155	1268	0	42	1445	243

in both *Agrostio-Caricetum* and *Succisio-Molinietum,* which tolerate a much wider range of soil pH (Fig. 2).

Successional changes: The ordination of snail samples of collection sites (1-30) clearly indicates (Fig. 3) the suc-

Table II. The constant (above), subconstant (middle) and accesorial (below) species of the two plant communities (*Succiso-Molinietum, Agrostio-Caricetum*) studied in more detail. K: constancy; D: dominance.
*Tabla II. Las especies constantes (arriba), subconstantes (medio) y accesorias (abajo) en las dos comunidades vegetales estudiadas (*Succiso-Molinietum, Agrostio-Caricetum*). K: constancia; D: dominancia.*

Succiso - Molinietum	**K**	**D**	***Agrostio - Caricetum***	**K**	**D**
Monacha carthusiana	100	9.32	*Chondrula tridens*	100	25.93
Succinea oblonga	90.9	15.91	*Monacha carthusiana*	100	13.03
Cochlicopa lubricella	81.81	17.32	*Succinea oblonga*	80	8.68
Vallonia enniensis	72.72	36.72	*Pupilla muscorum*	73.33	21.99
Chondrula tridens	72.72	12.72			
Vertigo pygmaea	45.45	1.88	*Vertigo pygmaea*	33.33	2.94
Carychium minimum	27.27	0.47	*Vallonia pulchella*	26.66	3.67
Vallonia pulchella	18.18	3.76	*Cepaea vindobonensis*	20	0.4
Cochlicopa lubrica	18.18	0.28	*Helix pomatia*	13.13	0.13
Carychium tridentatum	9.09	0.75	*Granaria frumentum*	6.66	5.74
Perforatella rubiginosa	9.09	0.28	*Vallonia costata*	6.66	0.53
Cepaea vindobonensis	9.09	0.09	*Cochlicopa lubricella*	6.66	0.26
Deroceras laeve	9.09	0.09	*Truncatellina cylindrica*	6.66	0.2
Deroceras sturanyi	9.09	0.09	*Helicopsis striata*	6.66	0.06
Malacolimax tenellus	9.09	0.09	*Zonitoides nitidus*	6.66	0.06
Pupilla muscorum	9.09	0.09			
Vertigo antivertigo	9.09	0.09			

cessional and zonational relationships of the plant associations studied, and a gradual habitat drying (BAGI, 1988). The main lines of the drying processes can be outlined as follows: (A) Non-salinic, wet line *Caricetum acutiformis-ripariae* (I, 1), *Succiso-Molinietum typicum* (II, 2-10), *S. -M. poetosum* (X, 11), *S. -M. agrostietosum* (XI, 12). The latter is a connection to a different, saline line: (B) *Bolboschoenetum maritimae* (IV, 14), *Agrostio-Caricetum bolboschoenetum* (IV, 21), *A. -C. fac. Juncus* (III, 16), *Agrostio-Caricetum plantaginetosum maritimae* (V, 17-20). Later, while the drying procces continues, the two lines originated a common line (C), whose representative associations are *A-C. festucetosum arundinaceae* (VI, 28), *A. -C. poetosum* (VIIa, 22-24), *A. -C. festucetosum pseudovinae* (VIII, 15) and finally the *Achilleo-Festucetum pseudovinae* (IX, 29). Roman numbers indicates groups of collection sites with similar features obtained from the analysis. The successionally closely connected plant communities often form zonation systems in the field. The drying processes have been particularly accelerated since the sixties, due to the draining of the region. The three successionally related lines could be distinguished in the process of draining-generated habitat drying by investigation of snails, too. The declining density of dead shells and living individuals, the fall of individual density (ID) and diversity (H') indicate habitat drying (X, V, VIIa, b, IX and VIII) and sometimes salinization (Fig. 4). Habitat drying accelerates with draining, which then leads to higher snail abundance again at the end of the successional xero-series at dry localities (*Achilleo-Festucetum* association). *Chondrula* and *Pupilla* can become especially numerous.

Snail species groups were used to evaluate these processes, for which the

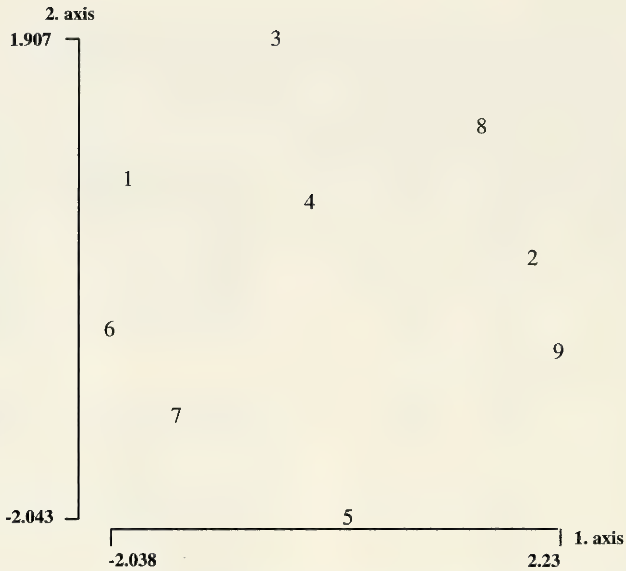

Figure 1. Distribution of constant and subconstant species according to soil pH (standardized PCA). 1: *Carychium minimum*; 2: *Succinea oblonga;* 3: *Cochlicopa lubricella*; 4: *Vertigo pygmaea*; 5: *Pupilla muscorum*; 6: *Vallonia costata*; 7: *Vallonia pulchella*; 8: *Vallonia enniensis*; 9: *Chondrula tridens.*
Figura 1. Distribucion de las especies constantes y subconstantes de acuerdo con el pH del suelo (Análisis de componentes principales estandarizado). 1: Carychium minimum*; 2:* Succinea oblonga*; 3:* Cochlicopa lubricella*; 4:* Vertigo pygmaea*; 5:* Pupilla muscorum*; 6:* Vallonia costata*; 7:* Vallonia pulchella*; 8:* Vallonia enniensis*; 9:* Chondrula tridens.

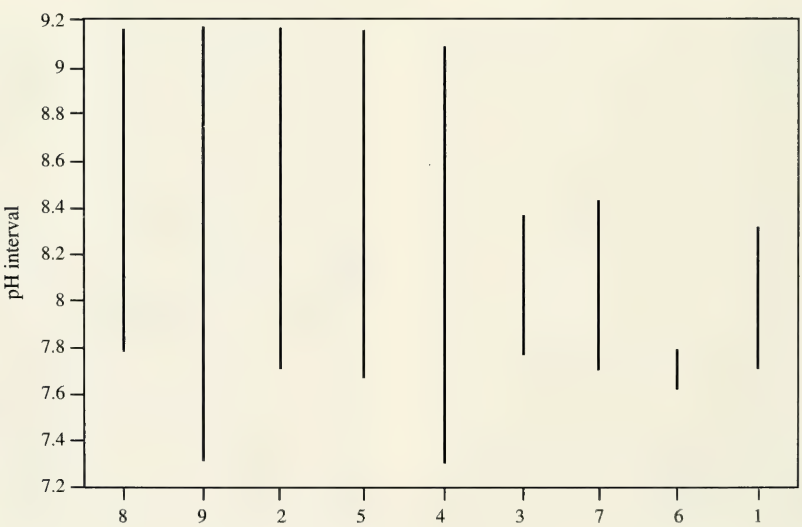

Figure 2. Distribution of the pH tolerance ranges of constant and subconstant species. Numbers refer to species as in Figure 1.
Figura 2. Distribución de los rangos de tolerancia al pH de las especies constantes y subconstantes. Los números de las especies son idénticos a los de la Figura 1.

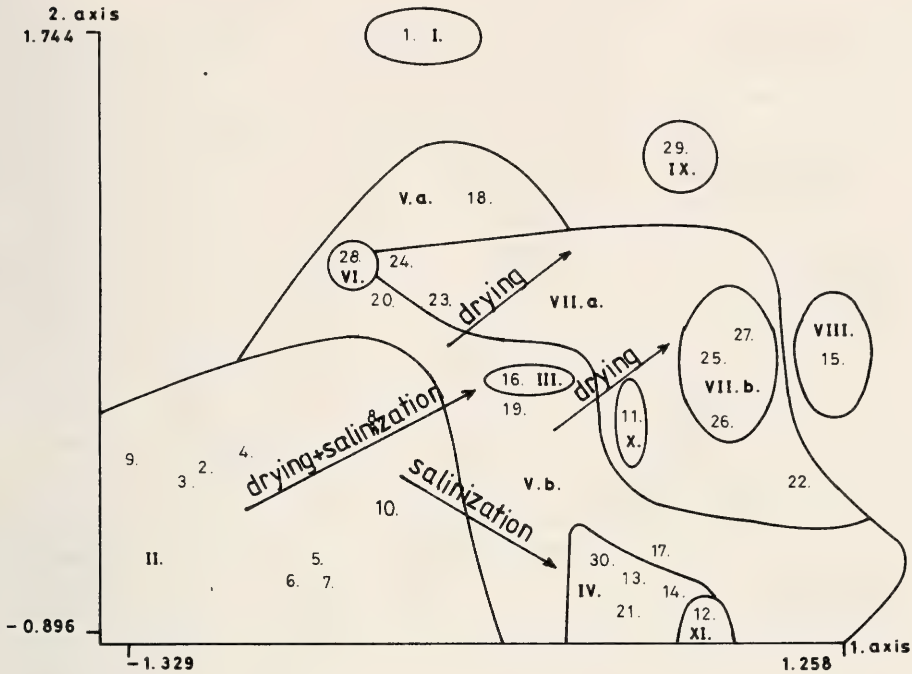

Figure 3. Ordination of collection sites by using data of snails samples (standardized PCA). Roman numbers indicate sample groups with similar phytological and malacological features; groups obtaines by ordination of data. Arabic numerals in brackets indicate collection sites. *Caricetum acutiformis-ripariae* I (1); *Succiso-Molinietum* a. *typicum* facies *Veratrum album* II (9), b. *typicum* facies *Phragmites* II (10), c. *typicum normale* II (2-8), d. *poetosum angustifoliae* X (11), e. *agrostietosum* XI (12); *Bolboschoenetum maritimae* IV (14); *Astero - Agrostietum* IV (30); *Agrostio - Caricetum distantis*, a. *agrostietosum* IV (13), b. *agrostietosum* facies *Juncus compressus* III (16), c. *plantaginetosum maritimae* Va, b (17-20), d. *poetosum angustifoliae* VIIa (22-24), e. *festucetosum arundinaceae* VI (28), f. *festucetusum pseudovinae* VII (15), g. *bolboschoenetosum* IV (20); *Achilleo - Festucetum pseudovinae* IX (29). See the text for further details.

Figura 3. Ordenación de las estaciones de muestreo utilizando datos de muestras de moluscos (Análisis de componentes principales estandarizado). Los números romanos indican grupos de estaciones con similares características fitológicas y malacológicas; los grupos se obtuvieron por ordenación de los datos. Los números arábigos entre paréntesis indican las localidades de muestreo. Caricetum acutiformis-ripariae *I (1);* Succiso-Molinietum *a.* typicum *facies* Veratrum album *II (9), b.* typicum *facies* Phragmites *II (10), c.* typicum normale *II (2-8), d.* poetosum angustifoliae *X (11), e.* agrostietosum *XI (12);* Bolboschoenetum maritimae *IV (14);* Astero *- NIV (30);* Agrostio - Caricetum distantis, *a.* agrostietosum *IV (13), b.* agrostietosum *facies* Juncus *NIII (16), c.* plantaginetosum maritimae *Va, b (17-20), d.* poetosum angustifoliae *VIIa (22-24), e.* festucetosum arundinaceae *VI (28), f.* festucetusum pseudovinae *VII (15), g.* bolboschoenetosum *IV (20);* Achilleo - Festucetum pseudovinae *IX (29). Véase el texto para más detalles.*

abundantial changes are shown (Figs. 5, 6, 7). Habitat drying and salinization have different consequences in the two plant associations. In the *Succiso-Molinietum* one, the abundance of riparian ubiquists (R, RU) monotonously decreases (collection sites 11 and 12 represent stages of ramification in the successional series). As the wet terrain dries down gradually, the abundance of species typical

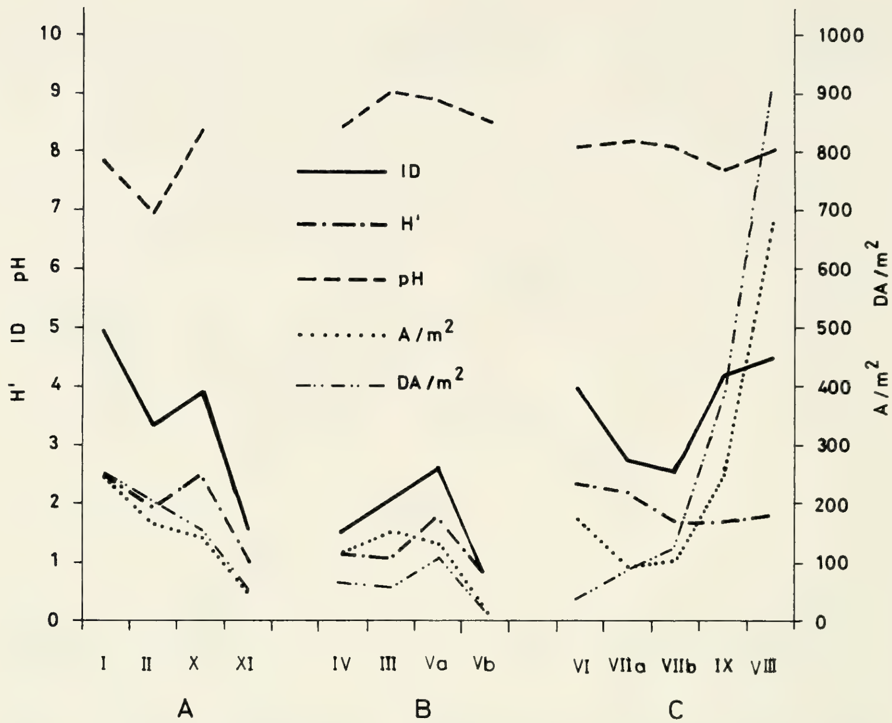

Figure 4. Variation in species density (ID), species diversity (H'), pH and density of living (A/m^2) and dead individuals (DA/m^2) in groups of phytocoenologically similar samples (Roman numerals) influenced by the dominant process of the habitat changes. A, B and C refer to the three succession lines of the vegetation. A includes groups I, II, X and XI; the main processes are drying (I, II and X) and salinization (XI). B includes groups IV, III and V; the main processes are drying (IV and III) and an additional salinization with cutting (Va, 18-20) and degradation (Vb, 17). C includes groups VI, VII, VIII and IX; the main processes are drying (VI, VIIa 22-24 and IX) with cutting (VIIb 25-27) and drainage (VIII).

Figura 4. Variación en la densidad de las especies (ID), diversidad (H'), pH y densidad de individuos vivos (A/m^2) y muertos (DA/m^2) en los grupos de muestras con características fitocoenológicas similares (números romanos) influenciadas por los procesos dominantes en los cambios de hábitat. A, B y C se refieren a las tres líneas de sucesión de la vegetación. A incluye los grupos I, II, X y XI; los principales procesos son la desecación (I, II y X) y la salinización (XI). B incluye los grupos IV, III y V; los principales procesos son la desecación (IV y III) y una salinización adicional con el segado (Va, 18-20) y degradación (Vb, 17). C incluye los grupos VI, VII, VIII y IX; los procesos principales son la desecación (VI, VIIa 22-24 y IX) junto con el segado (VIIb 25-27) y el drenaje (VIII).

in open areas (OA, ST) decreases, paralleled by a similar decline in the number of species and individuals (Figs. 5, 6). Concerning ecological species groups, the abundance of swamp dwellers (P, HP, *Monacha*) becomes higher with biotope salinization (12). Na^+ accumulation in the topsoil is responsible for its muddy character.

Sciophilous (S) and bush forest dweller (B) snail species may also appear in the tall and dense stands of *Caricetum acutiformis-ripariae* community. The abundance of OA and ST species groups increases at the end of the successional series in *Agrostio-Caricetum* and *Achilleo-Festucetum* associations. Groups P and HP are also more abundant there, due to

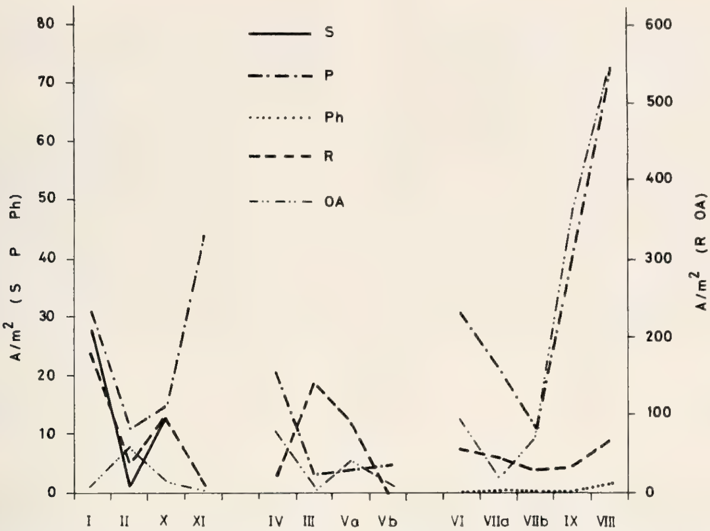

Figure 5. Variation in the abundance (A/m^2) of ecological snail species groups among plant associations and subassociations. Abbreviations, S: sciophilous, P: swamp dweller, Ph: photophilous, R: riparian and OA: species of open areas.

Figura 5. Variación en la abundancia (A/m^2) de los grupos ecológicos de especies de moluscos en el conjunto de las asociaciones y subasociaciones vegetales. Abreviaturas, S: esciófilo; P: de marisma; Ph: fotófilo; R: ribereño; OA: de áreas abiertas.

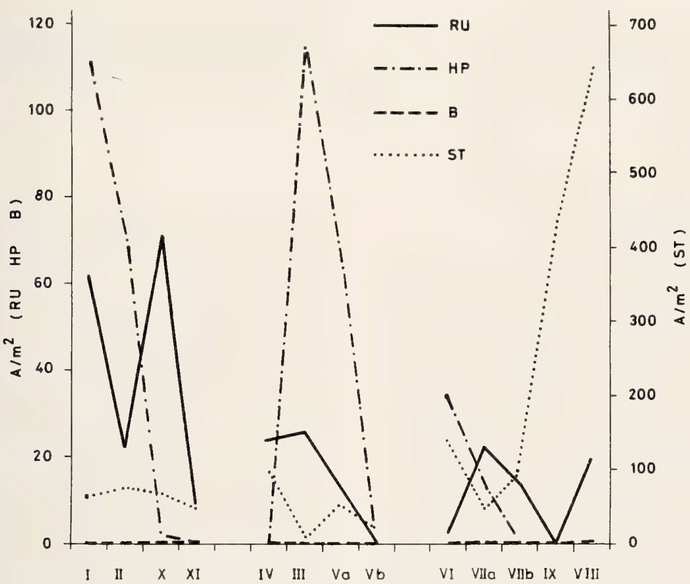

Figure 6. Variation in the abundance (A/m^2) of snail habitat type groups among plant associations and subassociations. Abbreviations, RU: riparian ubiquist, B: bush forest dweller, HP: hygrophilous swamp dweller and ST: steppe dweller.

Figura 6. Variación en la abundandia (A/m^2) de los tipos de hábitat en las especies de moluscos en el conjunto de las asociaciones y subasociaciones vegetales. Abreviaturas, RU: ribereño ubiquo; B: zonas arbustivas; HP: marismeño higrófilo; ST: estepa.

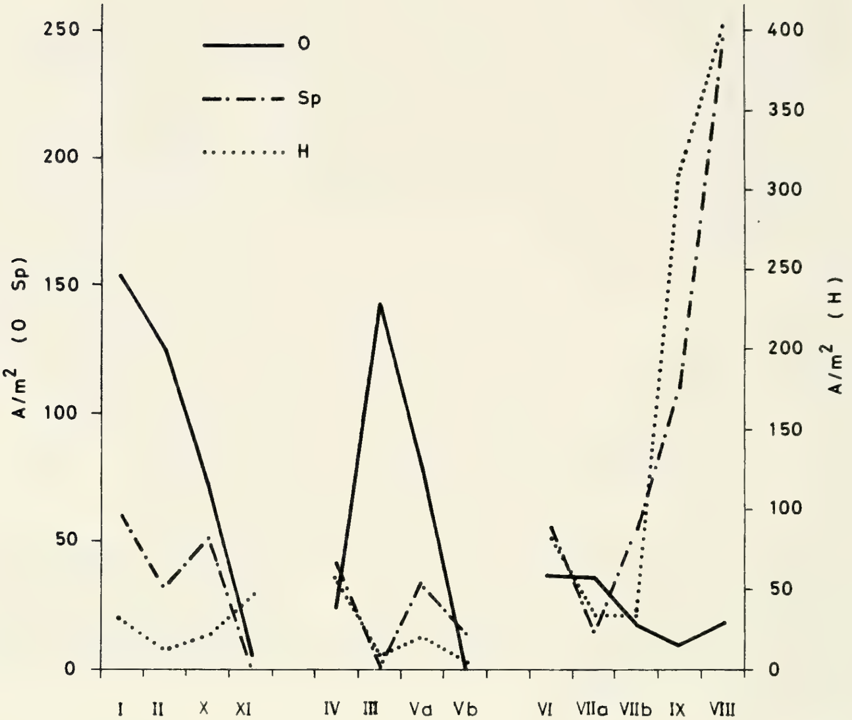

Figure 7. Variation in the abundance (A/m^2) of snail nutritional type groups among plant associations and subassociations. Abbreviations, O: omnivore, SP: saprophagous, H: herbivore.
Figura 7. Variación en la abundancia (A/m^2) de los grupos nutricionales de moluscos en el conjunto de las asociaciones y subasociaciones vegetales. Abreviaturas, O: omnívoro, SP: saprófago, H: herbívoro.

the muddy topsoil formed under Na^+ accumulation (Figs. 5, 6).

In both collection site groups of the *Agrostio-Caricetum* association, habitat salinization and drying, grazing and cutting result in the decline of the proportion of riparian ubiquists (R, RU: *Succinea, Vallonia pulchella*), and a complementary increase in the abundance of steppe dwellers (OA, ST: *Chondrula, Pupilla*). Stands of XI, Va and VIIa are regularly cut, while site of VIII is both cut and drained (Figs. 5, 6).

In terms of nutritional types, omnivorous snail species dominate in each collection site group, as it was also found elsewhere in willow-poplar forests (Bába, 1993). With habitat drying the vegetation becomes denser, resulting in a higher abundance of herbivores. Subsequent cutting increases the proportion of saprophagous species (*Vallonia, Chondrula, Vertigo*). The omnivore and herbivore-saprophagous groups were found to change in a complementary manner (Fig. 7).

According to our data, the connection between the vegetation units and the species groups of snails seems to be very close. The composition of snail assemblages indicates the most important environmental changes, such as drying and salinization, and the human impacts, eg. cutting, mowing and some other disturbances. The structural transformation of snail assemblages can be followed at a level of species groups and also within these groups. The snail assemblages indicate not only the differences between plant communities but the diffe-

rent impacts of natural and anthropogenic factors within a plant community as well. The consequences of the habitat drying are the decrease in species number and increase in abundance; the salinization causes the decrease of species number and change of species groups in a particular habitat. Mowing leads to the decrease of species number and increase of the ratio of saprophagous and steppe dweller species groups. The changes can be traced back to pedological reasons, eg. habitat drying, increase in pH value, and accumulation of organic matter. The investigations of the structural and compositional changes of snail assemblages of the studied six plant communities may provide a way to detect the consequences of the salinization as a characteristic successional process of Hungarian Great Plain. The studies on the changes of snail assemblages in meadow plant communities can indicate the main processes in this vegetatation type similar to the investigations carried in forest ecosystems (Bába, 1993).

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Morphological and biometrical researches on Austrian Clausiliids. Shell morphology and variability in *Clausilia dubia* Draparnaud, 1805

Investigaciones biométricas y morfológicas en Clausílidos de Austria. Morfología y variabilidad de la concha de *Clausilia dubia* Draparnaud, 1805

Karl EDLINGER*

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ABSTRACT

Morphological and biometrical studies on shells of some Austrian populations of *Clausilia dubia* Draparnaud, 1805, show a great variability in size and in the other morphological features within the species as a whole and also within single populations. Investigations of the variability of characters by metrical and statistical methods in some populations disclose impressive metrical divergences and morphological differences.

These results give rise to the question whether the characterization of *Clausilia dubia* as a polytypic species, as suggested by KLEMM (1960, 1973), is justified.

RESUMEN

Estudios morfológicos y biométricos en conchas de algunas poblaciones austríacas de *Clausilia dubia* Draparnaud, 1805, muestran una gran variabilidad en el tamaño y en otros caracteres morfológicos tanto en el conjunto de la especie como en poblaciones aisladas. Investigaciones sobre la variabilidad de caracteres por medio de métodos métricos y estadísticos de algunas poblaciones mestran importantes divergencias tanto métricas como morfológicas.

Estos resultados originan la pregunta de si está justificada la caracterización de *Clausilia dubia* como una especie politípica, como sugiere KLEMM (1960, 1973).

KEY WORDS: *Clausilia dubia*, subspecies, measures, distribution, morphological continuum.
PALABRAS CLAVE: *Clausilia dubia*, subespecies, medidas, distribución, continuidad morfológica.

INTRODUCTION

As in great parts of Europe also in Austria, specially in the eastern parts of the Alps and in the adjacent areas, *Clausilia dubia* Draparnaud 1805 is a widely diffused and in some localities a common species that is believed to be polytypic (KLEMM, 1960, 1973; FECHTER AND FALKNER, 1990; KEARNEY, CAMERON AND JUNGBLUTH, 1983; NORDSIECK, 1990). KLEMM (1960, 1973) gave a survey of di-

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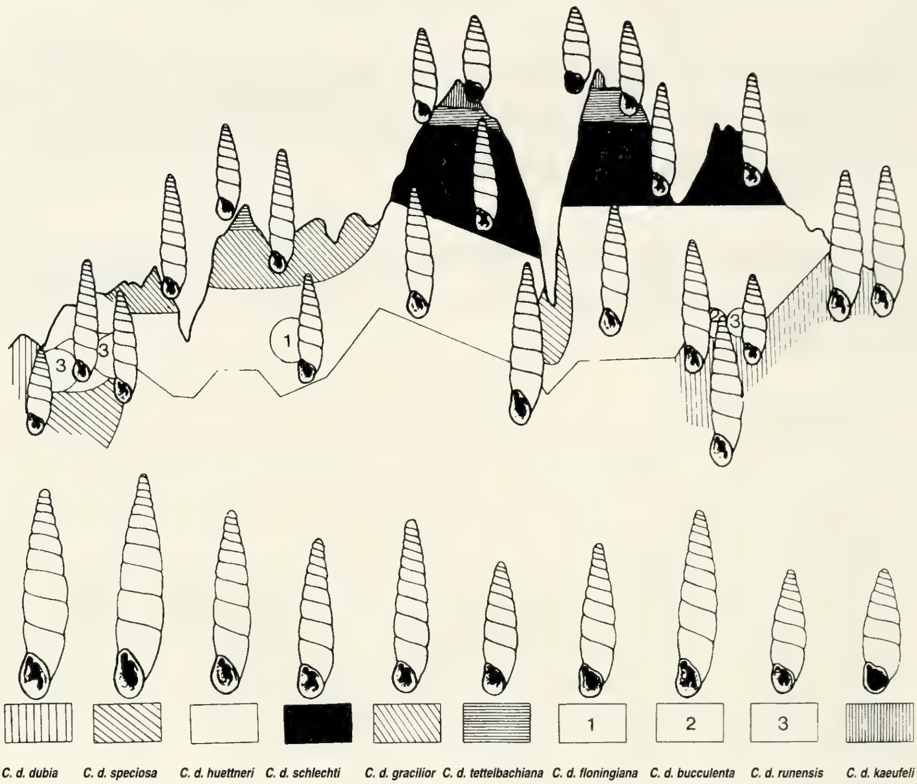


Figure 1. Distribution and vertical succession of *Clausilia dubia* subspecies as is suggested by KLEMM (1960).
Figura 1. Distribución y sucesión vertical de las subespecies de Clausilia dubia, *tal y como sugiere KLEMM (1960).*

verse "subspecies" of *Clausilia dubia* according to the characters suggested by several authors.

Traditional classification was based on a subjective selection of characters believed to be important. This classification depended on the preferences of the single authors. In some cases, subspecies are even described according to the presence of typical features in the shell of few or single specimens. HOLOYAK AND SEDDON (1988) and NORDSIECK (1990) examined some of these descriptions and offered reasonable revisions.

Some of these *Clausilia dubia* "subspecies" are considered to be widely distributed, others to be localized in small areas or subdivided into isolated populations that live in separated sites (KLEMM, 1960, 1973). Furthermore, KLEMM (1960) suggested a vertical pattern of distribution and an altitude dependent succession of diverse subspecies at the eastern ranges of the Alps (Fig. 1). He tried to explain the observed distribution pattern by probable re-immigration events in the alpine region after the Pleistocene and adaptation, enforcing the role of the environment (altitude).

Examination and possible revision of these interpretations have to critically consider the definition and the meaning of the term subspecies as it is used under various perspectives by several authors. For the practical requirement of the collector and for the taxonomic ordering of collections the technical term "subspecies" as based on peculiar morphological features

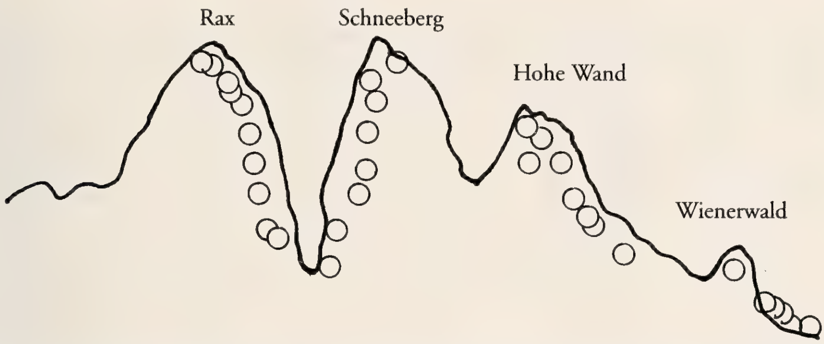


Figure 2. A profil of the estern edge of the Alps and the Wienerwald with the sample localities.
Figura 2. Perfil de la cara este de los Alpes y del Wienerwald con las localidades de muestreo.

may certainly be useful. However, it is scientifically more important to consider the conceptual background of the terminology. In the given context the concept of race or subspecies refers to biological units that are groups of related populations which are genetically characterized and, in the case of very long isolation, may be the forerunners of "valid species" (MAYR, 1967: 387; SUDHAUS AND REHFELD, 1992). This view is highly important for traditional evolutionary biology, especially in the frame of Darwinian models for evolutionary change.

In respect to the biological relevance of the subspecies concept, Sudhaus and REHFELD (1992) are suggesting that "geographic races" (subspecies) are allopatric populations of a species, which can be distinguished taxonomically. The diagnostic characters of races should be present in 90 or more percent of individuals of the population. "

OSCHE (1994) claims that 75 percent or more members of a population must be morphologically distinguishable from the members of another population. Populations only in this case should be accepted as valid subspecies. In this paper Osche´s definition is assumed as a very tolerant and useful concept.

According to the presuppositions just given, studies referring to the subspecies problem have to treat large numbers of individuals and to apply methods of greater exactness than the usual descriptions and discriminations of characters based on a subjective and rather arbitrary approach. It is therefore necessary to study as great a number as possible of morphological characters and to take measurements of the greatest possible exactness to establish a solid basis for statistical evaluations (NEMESCHKAL AND KOTHBAUER, 1988; KOTHBAUER, NEMESCHKAL, SATTMANN AND WAWRA, 1991; NEMESCHKAL, 1990, 1991, 1993; MYLONAS, KRIMBAS, TSIAKAS AND AYOUNTANTI, 1990).

Such investigations may clear up, whether the populations studied by Klemm meet all requirements of a reliable identification as subspecies (EDLINGER AND FISCHER, 1997). It is also worth while to attempt a critical revision of some samples of the Museum of Natural History in Vienna (NHMW). This paper is first attempt at elaborating a new basis for the discussion of the *Clausilia dubia* problem by morphological measurements. In future the anatomy of the soft parts and genetical analyses might be also considered.

MATERIAL AND METHODS

606 specimens of *Clausilia dubia* from different lots collected in various areas of the "Wienerwald" (Lower Austria in the southwest of Vienna) the massif of the "Hohe Wand", the "Schneeberg" and the "Rax" were investigated. The localities from which the samples came were situated at altitudes between 270 and 1850 m (Fig. 2).

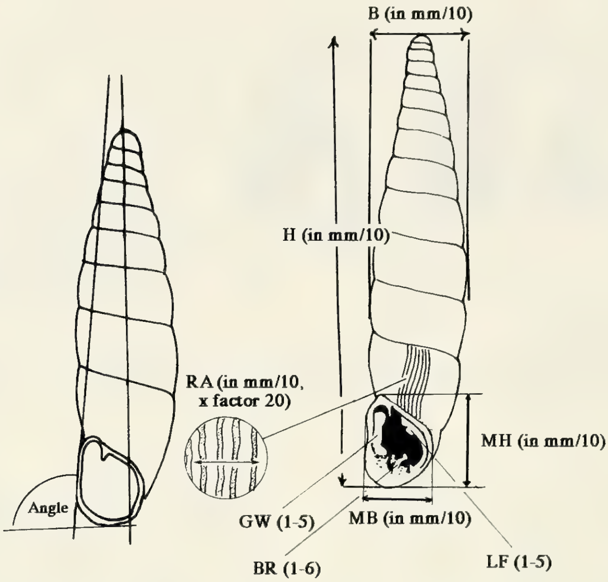


Figure 3. Measures taken from the shells: shell-height (H), shell-width (B), height (MH) and width (MB) of the aperture, distance of ribs (RA), number of whorls (WZ), angle between the spindle axis and the upper palatal (left side) (A).
Figura 3. Medidas tomadas en las conchas: altura (H), anchura (B), altura (MH) y anchura(MB) de la apertura, distancia de las estrías (RA), número de vueltas (WZ), ángulo entre el eje del huso y palatal superior (lado izquierdo) (A).

Samples (Number of Sample (Sample localities, altitude / numbers of specimens. R = Rax: R4 (Reichenau, 700 m / 1 spec.), R5 (Aufstieg z. Knappenhof, 730 m / 5 spec.), R7 (Knappenhof, 800 m / 24 spec.), R10 (Thörlweg, 850 m / 5 spec.), R11 (Thörlweg, 960 m / 1 spec.), R12 (Thörlweg, 1120 m / 29 spec.), R13 (Thörlweg, 1260 m / 20 spec.), R14 (Thörlweg, 1320 m / 12 spec.), R15 (Jakobskogel, 1685 m / 8 spec.); S = Schneeberg: S1 (Puchberg, 560 m / 15 spec.), S2 (Schneebergbahn, 750 m / 57 spec.), S3 (Schneebergbahn, 790 m / 5 spec.), S4 (Schneebergbahn, 945 m / 30 spec.), S5 (Schneebergbahn, 1165 m / 9 spec.), S6 (Schneebergbahn, 1370 m / 6 spec.), S8 (Waxriegl ll, 1820 m / 4 spec.), S9 (Waxriegl ll, 1850 m / 26 spec.), S10 (Schneebergbahn, 1650 m / 11 spec.), H = Hohe Wand: H1 (Dreistetten, 530 m / 60 spec.), H2 (Einhornhöhle, 600 m / 12 spec.), H3 (Drobilsteig, 700 m / 24 spec.), H4 (Drobilsteig, 760 m / 69 spec.), H5 (Auffahrt z. Plateau, 830 m / 74 spec.), H6 (Plateau 1020 m / 6 spec.), H7 (Plateau 1020 m / 34 spec.), H8 (Plateau 1020 m / 4 spec.); W = Wienerwald: W1 (Anninger, 400 m / 11 spec.), W2 (Anninger, 450 m / 4 spec.), W3 (Mödling-Klause, 260 m / 8 spec.), W4 (Husarentempel, 480 m / 14 spec.), W5 (Aufgang Anninger, 270 m / 11 spec.), W6 (Peilstein, 400 m / 8 spec.),

Several individuals were dissected. Dissections did not reveal significant differences in the genital apparatus. 18 shells, syntypes of Austrian and South Tyrolean (Italy) localities, given in loan by the Natur-Museum Senckenberg as typical representatives of various subspecies were used for comparisons (Fig. 1).

They are:

1. *Clausilia dubia dubia* Draparnaud, 1805 (SMF 163024a)
2. *Clausilia dubia speciosa* A. Schmidt, 1857 (SMF 163025a)
3. *Clausilia dubia speciosa* A. Schmidt, 1857 (SMF 163026a)
4. *Clausilia dubia obsoleta* A. Schmidt, 1857(SMF 163027a)

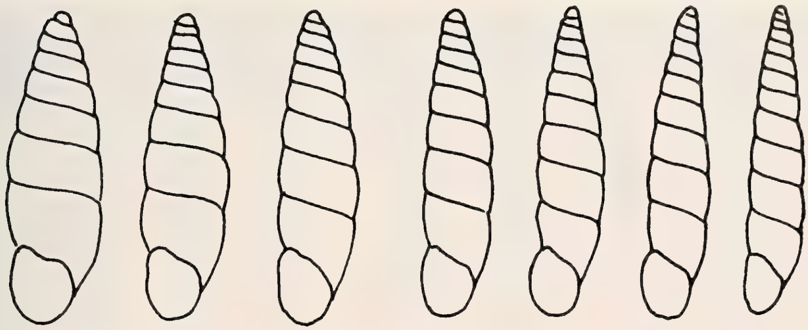


Figure 4. Shell forms (7 stages from club-shaped -left- to spindle-shaped -right-).
Figura 4. Formas de la concha (siete estadios desde forma de maza -izquierda- hasta ahusada -derecha-).

5. *Clausilia dubia huettneri* Klemm, 1960 (SMF 1630248)
6. *Clausilia dubia schlechti* A. Schmidt, 1857 (SMF 163030a)
7. *Clausilia dubia gracilior* Clessin, 1887 (SMF 163031a)
8. *Clausilia dubia tettelbachiana* Rossmässler, 1838 (SMF 163032a)
9. *Clausilia dubia otvinensis* H. Gallenstein, 1895 (SMF 163033a)
10. *Clausilia dubia grimmeri* L. Pfeiffer, 1848 (SMF 163034a)
11. *Clausilia dubia floningiana* Tschapek, 1886 (SMF 163035a)
12. *Clausilia dubia floningiana/gracilior* (SMF 163036)
13. *Clausilia dubia bucculenta* Klemm, 1960 (Holotypus, SMF 163037)
14. *Clausilia dubia runensis* Tschapek, 1883 (SMF 163039a)
15. *Clausilia dubia moldanubica* Klemm, 1960 (Holotypus, SMF 163040)
16. *Clausilia dubia kaeufeli* Klemm, 1960 (Holotypus, SMF 163042)
17. *Clausilia dubia alpicola* Clessin, 1878 (SMF 31969)
18. *Clausilia dubia reticulata* Pini, 1883 (SMF 31936)

The shells were measured under a binocular microscope; the measurements were repeated three times. In the case of different results a special check was made. The height (H, Fig. 3) and the width (B, Fig. 3) of the shell as a whole, the height (MH, Fig. 3) and the width (MB, Fig. 3) of the aperture, the form of the aperture (MF, a series of 9 stages from pear-shaped to deltoid form, the angle between the spindle axis and the edge of the upper palatal (0.5 degree exactness), the mean of 5 rib distances (RA, Fig. 3) on the last whorl, and the number of whorls per shell (WZ, exactness: 0.25) were recorded. By comparison with stencils the morphological characters of the form of the shells (GH, a series of 7 stages from club-shaped, to extremely spindle-shaped specimens, Fig 4), the depth, and the thickness of the basal groove (BR, 6 stages, Fig. 5), the lateral internal bulge (GW, on the left side of the aperture, 5 stages of thickness (Fig. 5), and the incision in the columellar lamella (LF, 5 stages, Fig. 5) were recorded.

The measured values of the following features were processed by a WINDOWS-EXCEL 5.0 and a WINDOWS SPSS 6.0 program (BROSIUS AND BROSIUS, 1995):

- Mean of shell heights in each spot check
- Standard deviation of shell heights in each spot check
- Mean of shell heights in each spot check
- Standard deviation shell heights in each spot check
- Correlation (Pearson´s) Coefficient of all 11 values:

$$R = \frac{\sum_{i=1}^{N}\left(X_i - \bar{X}\right)\cdot\left(Y_i - \bar{Y}\right)}{(N-1)\cdot S_x \cdot S_y}$$

Figure 5. Basal groove (6 stages, upper row); lateral bulge (5 stages, middle row); incision in the columellar lamella (5 stages, lower row).
Figura 5. Surco basal (6 estadios, arriba); protuberancia lateral (5 estadios, centro); incisión en la lamela columelar (5 estadios, abajo).

(R= Pearson´s Coefficient; N= number of cases; X, Y= variables; Sx, Sy= standard deviation of the variables).

By means of the WINDOWS SPSS 6.0 programs a factor extraction and a principle component analysis were executed. "Community" delivers information about the quota of spreading of one value that can be traced back to all other values. "Eigenvalue" is a value of the regression factors. It represents the quota of spreading of all values as interpreted by special regression factors. A reduction process restricts the numbers of factors in the final statistics to that exceeding 1.0. The factor matrix shows the influence of the regression factors on every variable as a percentage of 1.

The measured variables of the samples in conjunction with the values of the specimens described by KLEMM (1960) and the values of specimens of *Clausilia dubia alpicola* and *C. d. reticulata* were utilized for computing hierarchical clusters as dendrograms. For purpose of cluster analysis the measured values were transformed to "z-values", values with a mean of 0 and a standard deviation of 1. Hierarchical clusters result from dissimilarities computed on the basis of the sums of squared values of distances of each character. Thereby the spectrum of similarities and differences between all individuals of a spot check could be elaborated. The dendrograms contain specimens of various clusters according to their graduated similarity (BROSIUS AND BROSIUS, 1995).

The formula of the general distances:

$$D^2 = \sum_{i=1}^{\upsilon} \left(X_i - Y_i\right)^2$$

(D= distance; υ= number of variables; X, Y= cases)

RESULTS

Means of shell height and shell width: The means of the shell height and shell width differ in all sampling areas. The lowest value was found at the "Hohe Wand" region, the highest in the "Wienerwald" area. Comparisons of the means at different altitudes reveal that KLEMM´s (1960) suggestion of a succession of different shell heights (according to a succession of "races" resp. subspecies, high values at low altitudes, low values at high altitudes) is not generally convincing (Fig. 7).

Figure 6. Two spot-checks of the collection of the NHMW (Naturhistorisches Museum, Wien). In the upper row "*Clausilia dubia schlechti*", Inv. Nr. 11. 229 NHMW. The specimen in the upper row at the left belongs to *Neostyriaca corynoides* (Held, 1836). In the row below *C. d.* "*schlechti*", Inv. Nr. 62. 348 NHMW. These spot-checks show us a high variability in the "subspecies". Scale bar 1 cm.
*Figura 6. Dos muestras de la colección del NHMW (Naturhistorisches Museum, Wien). En la fila superior "*Clausilia dubia schlechti*", Inv. Nr. 11. 229 NHMW. El especimen de la izquierda de la fila superior pertenece a* Niostyriaca corynoides *(Held, 1836). En la fila inferior* C. d. "schlechti", *Inv. Nr. 62. 348 NHMW. Las fotografías muetran una alta variabilidad en las subespecies. Escala 1 cm.*

Correlation coefficients: A very remarkable outcome of the study was a low positive correlation between the altitude and the shell height (Table I) but a high correlation between altitude and the incicion in the columellar lamella.

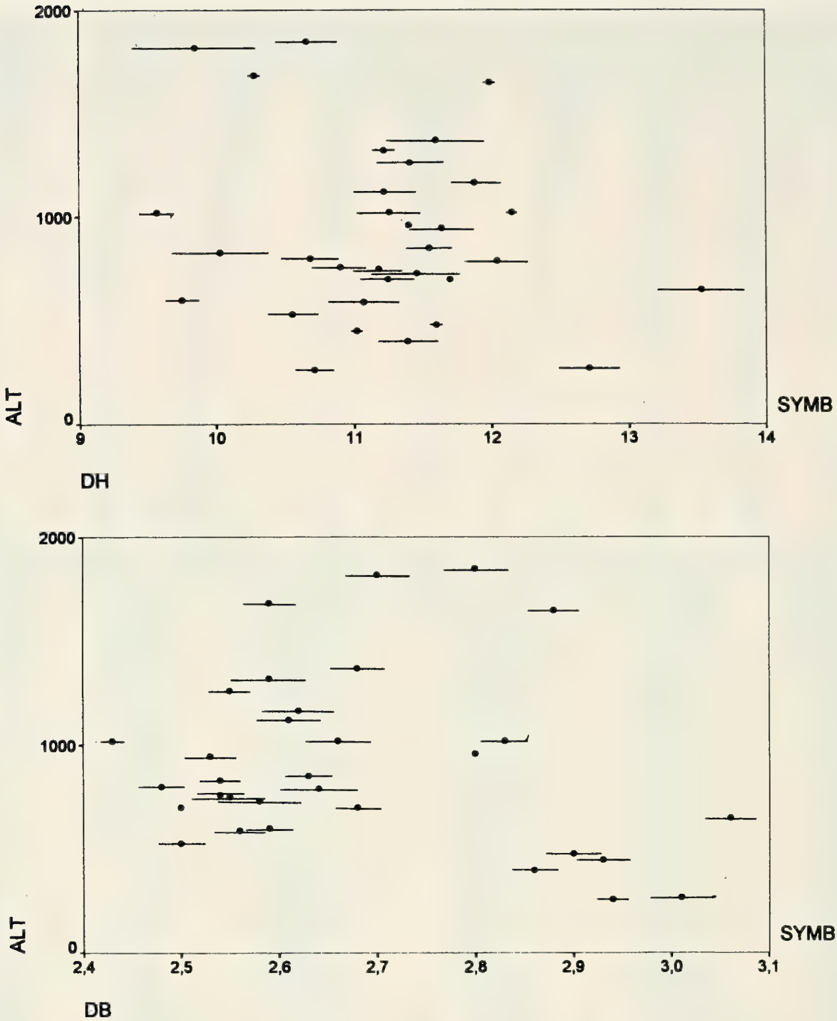


Figure 7. Scatter plots of the means of the height and width of the various samples and the altitude of sampling points.
Figura 7. Diagrama de puntos de las alturas y anchuras medias de las distintas muestras y la altitud de los puntos de muestreo.

In all four regions a significant correlation between the altitude and the height of the shells could not be confirmed. A maximum of correlation was found between shell height and the height of the aperture. Correlations between shell height and heigth of the aperture, shell height and number of whorls, shell form and number of whorls, shell form and shell height, shell height and width of the aperture, and between width of the shell and width of the aperture, are more or less remarkable. Correlation between altitude and most of the shell variables with the exception of the columellar lamella (negative correlation: -0.5123) is low (Table I).

Primary factor analysis: For the primary factor analysis all values were

Table I. Correlation coefficients (bivariate) of altitude (ALT), breadth (B), basal groove (BR), shell-form (GHF), internal bulge (GW), heighth (H), the incision in the columellar lamella (UL), width of aperture (MB), angle between the upper palatal and the spindle axis (A), height of the aperture (MH), distance of ribs (R) and number of whorls (WZ).
Tabla I. Coeficientes de correlación (bivariables) de altitud (ALT), anchura (B), surco basal (BR), forma de la concha (GHF), protuberancia interna (GW), altura (H), incisión en la lamela columelar (UL), anchura de la apertura (MB), ángulo entre el palatal superior y el eje del huso (A), altura de la apertura (MH), distancia entre las estrías (R) y número de vueltas (WZ).

	A	ALT	B	BR	GHF	GW
A	1.0000	-.0487	.1696**	.0493	.2272**	.0646
ALT	.0487	1.0000	-.0032	.1262**	-.0036	.2082**
B	.1696**	-.0032	1.0000	.1297**	.2510**	.0438
BR	.0493	.1262**	.1297**	1.0000	.0148	.3307**
GHF	.2272**	-.0036	.2510**	.0148	1.0000	.1171**
GW	.0646	.2082**	.0438	.3307**	.1171**	1.0000
H	.2011**	-.0021	.3814**	.1351**	.5258**	.1397**
LF	.0213	.5123**	.1453**	.2311**	-.0741	-.0542
MB	.0822*	.1590**	.4693**	.1606**	.0446	.1331**
MH	.0450	.0214	.5417**	.1644**	.0656	.1621**
R	.1370**	.1850**	.0931*	-.0704	.2172**	.1103**
WZ	.2812**	.1711**	.0127	.0745	.5760**	.0632

	H	LF	MB	MH	R	WZ
A	.2011**	.0213	.0822*	.0450	.1370**	.2812**
ALT	.0021	.5123**	.1590**	.0214	.1850**	.1711**
B	.3814**	.1453**	.4693**	.5417**	.0931*	.0127
BR	.1351**	.2311**	.1606**	.1644**	-.0704	.0745
GHF	.5258**	-.0741	.0446	.0656	.2172**	.5760**
GW	.1397**	-.0542	.1331**	.1621**	.1103**	.0632
H	1.0000	.0780	.4968**	.7071**	.1411**	.6663**
LF	.0780	1.0000	.2288**	.0913*	.1501**	.0891*
MB	.4968**	.2288**	1.0000	.5965**	-.0230	.1733**
MH	.7071**	.0913*	.5965**	1.0000	-.0412	.2455**
R	.1411**	.1501**	-.0230	-.0412	1.0000	.2058**
WZ	.6663**	.0891*	.1733**	.2455**	.2058**	1.0000

*= Signif. LE .05;**= Signif. LE .01 (2-tailed)

used irrespective of the altitude. The analyses result four factors with an Eigenvalue of more than 1.0. One analysis was done including the NMS specimens (Table II), the other only with the own samples (Table III). The results of both analyses were corresponding at a high degree.

Factor 1 has a significant influence on the width of the shell, the shell height, the width of the aperture, the height of the aperture and the number of whorls.

Factor 2 has a significant influence on the angle between the axis and the left palatal, the width of the aperture, the rib distance and the number of whorls, factor

Table II. Primary component analysis factors of all samples including the NMS specimens. Abbreviations as in Table I.

Tabla II. Factores del análisis de componentes principales de todas las mustras incluyendo los ejemplares NMS. Abreviaturas como en la Tabla I.

Initial Statistics

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
A	1.00000	1	3.14275	31.4	31.4
B	1.00000	2	1.48937	14.9	46.3
BR	1.00000	3	1.34787	13.5	59.8
GW	1.00000	4	1.09305	10.9	70.7
H	1.00000	5	.81589	8.2	78.9
LF	1.00000	6	.69772	7.0	85.9
MB	1.00000	7	.54068	5.4	91.3
MH	1.00000	8	.42572	4.3	95.5
R	1.00000	9	.32418	3.2	98.8
WZ	1.00000	10	.12276	1.2	100.0

PC extracted 4 factors

Factor Matrix

	Factor 1	Factor 2	Factor 3	Factor 4
A	.24107	-.39349	.57325	-.01561
B	.64730	.28942	-.49248	-.01712
BR	.19488	.59543	.52902	.22231
GW	.11069	.50354	.53469	-.34493
H	.89714	.19205	.07467	-.16390
LF	.25618	.22266	.08430	.85909
MB	.75790	.21202	-.17180	.03663
MH	. 85718	. 10931	-.19219	-.16564
R	.24758	.55811	.01044	.35599
WZ	.61193	-.43340	.36292	-.06089

Final Statistics

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
A	.54182	1	3.14275	31.4	31.4
B	.74559	2	1.48937	14.9	46.3
BR	.72179	3	1.34787	13.5	59.8
GW	.67067	4	1.09305	10.9	70.7
H	.87418				
LF	.86036				
MB	.65022				
MM	.81108				
R	.49962				
WZ	.69772				

Skipping rotation 1for extraction 1 in analysis 1

Table III. Primary component analysis factors of all samples excluding the NMS specimens. Abbreviations as in Table I.
Tabla III. Factores del análisis de componentes principales excluyendo los ejemplares NMS. Abreviaturas como en la Tabla I.

Initial Statistics

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct*
A	1.00000	1	2.98596	29.9	29.9
B	1.00000	2	1.52656	15.3	45.1
BR	1.00000	3	1.27032	12.7	57.8
GW	1.00000	4	1.19526	12.0	69.8
H	1.00000	5	.79324	7.9	77.7
LF	1.00000	6	.70682	7.1	84.8
MM	1.00000	7	.56029	5.6	90.4
MM	1.00000	8	.45357	4.5	94.9
R	1.00000	9	.36803	3.7	98.6
WZ	1.00000	10	.13995	1.4	100.0

PC extracted 4 factors

Factor Matrix

	Factor 1	Factor 2	Factor 3	Factor 4
A	.19408	.61541	.28529	-.11267
B	.60129	-.52606	-.27656	.02153
BR	.32508	-.17128	.64145	.42482
GW	.25481	-.15515	.76411	-.07054
H	.86917	.22511	-.06761	-.24429
LF	.28165	.05486	-.10404	.82738
MM	.74584	-.22587	-.11384	.04898
MM	.83214	-.22388	-.10785	-.18500
R	.18873	.53391	-.27470	.43010
WZ	.54499	.61465	.04084	-.17555

Final Statistics

Variable	Communality	Factor	Eigenvalue	Pct of Var	Cum Pct
A	.51047	1	2.98596	29.9	29.9
B	.71523	2	1.52656	15.3	45.1
BR	.72695	3	1.27032	12.7	57.8
GW	.67784	4	1.19526	12.0	69.8
H	.87038				
LF	.77771				
MM	.62266				
MM	.78843				
R	.58114				
WZ	.70730				

Skipping rotation 1 for extraction 1 in analysis 1

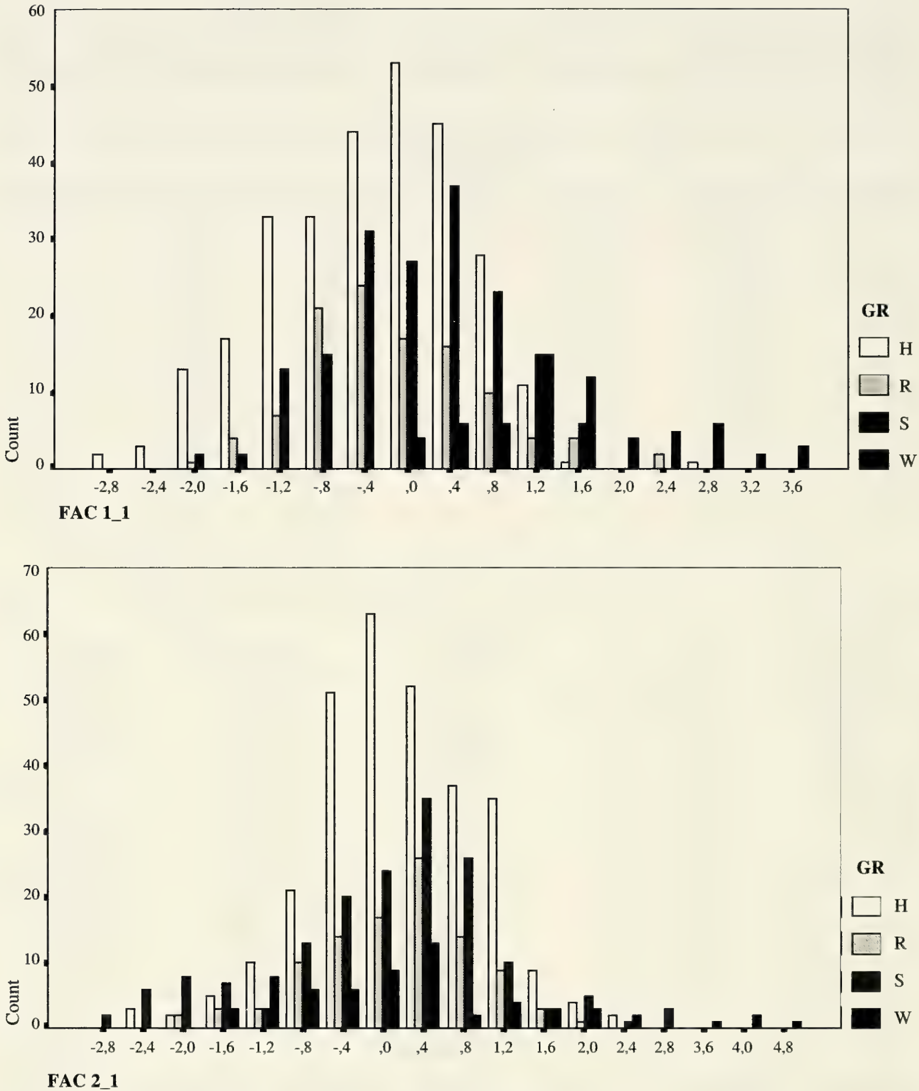


Figure 8. Bar charts of factor 1 and 2 (spot checks differentiated).
Figura 8. Diagrama de barras de los factores 1 y 2 (pruebas diferenciadas).

on the basal groove and factor 4 has a significant influence on the columellar lamella.

Bar charts show us the distributions and the maximum of the values of the primary factors in the samples for comparison.

The values of factor 1 have a similar distribution in the Schneeberg, the Rax and the Hohe Wand area and another distribution pattern with another maximum in the Wienerwald area (Fig. 8).

The values of factor 2 show us a very similar distribution in the Rax and the Schneeberg area, but other patterns in the Hohe Wand and the Wienerwald area (Fig. 8).

Factor 3 has similar distributions of values in the samples of Rax, Schneeberg

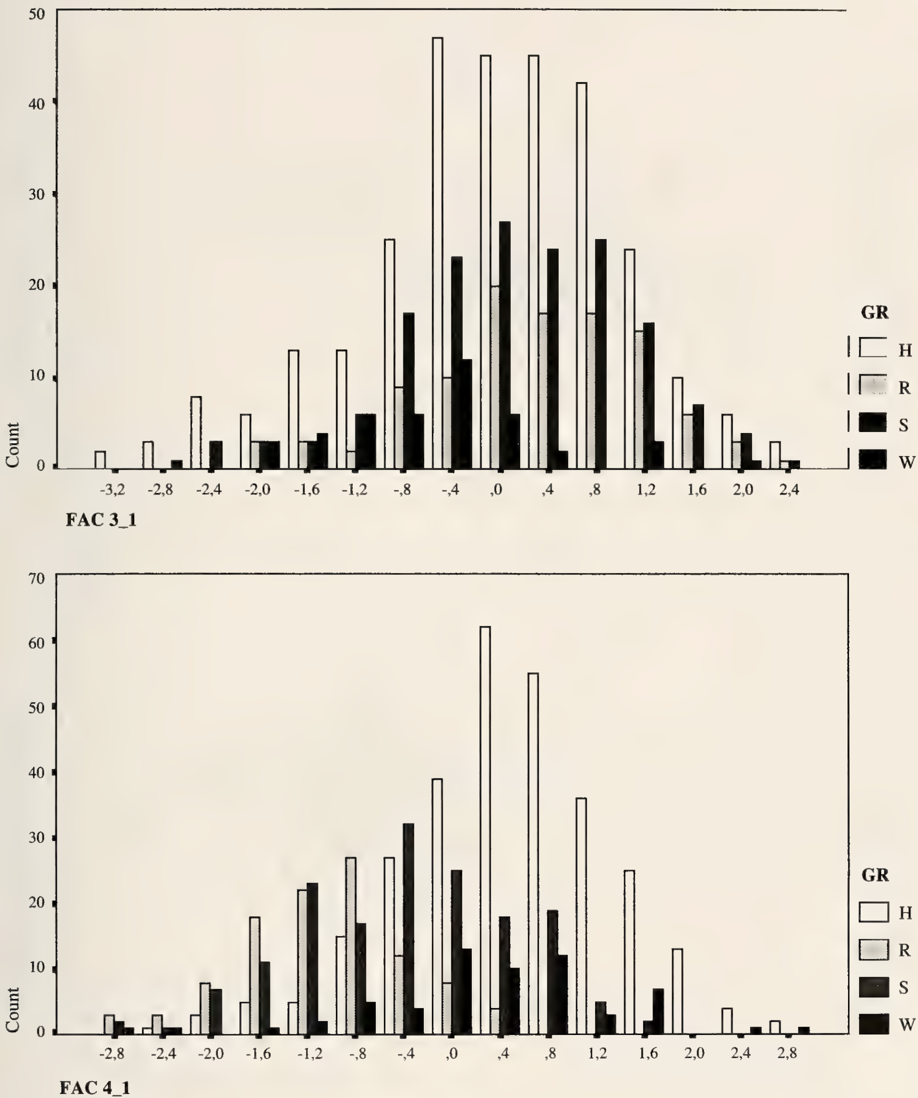
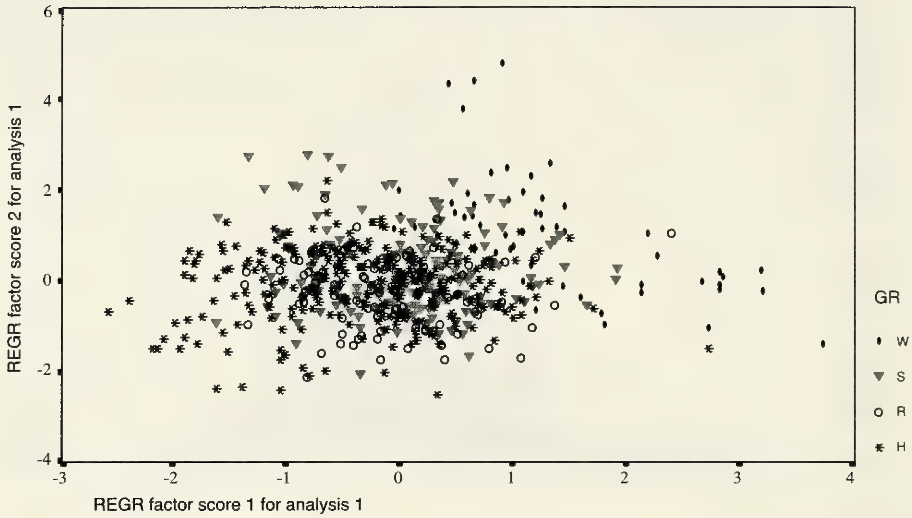


Figure 9. Bar charts of factor 3 and 4 (spot checks differentiated).
Figura 9. Diagrama de barras de los factores 3 y 4 (pruebas diferenciadas).

and Hohe Wand, but another maximum in the Sample of the Wienerwald area (Fig. 9).

Diagrams of the values of factor 4 show us different distributions in all samples (Fig. 9).

A two dimensional scatter plot of factor 1 and factor 2 for a comparison of the samples of the four areas (Fig. 10) shows us, that by the positions of the specimens and by their pattern of distribution only two partially different groups can be distinguished: one group consisting of specimens of the Hohe Wand, the Schneeberg and the Rax area at the one side and a second group with the specimens from the Wienerwald area at the other. Both groups are overlapping.



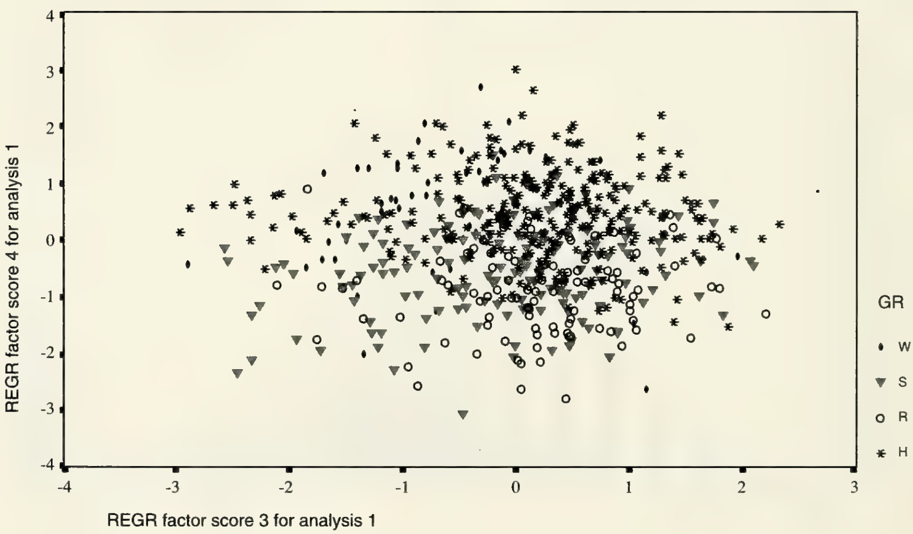


Figure 10. Scatter plots of the samples with value 1 and 2, 3 and 4 (spot checks differentiated).
Figura 10. Diagramas de puntos de las muestras con los valores 1 y 2, 3 y 4 (pruebas diferenciadas).

A scatter plot with factor 3 and factor 4 (Fig. 10) shows us a wide distribution of the specimens of the Schneeberg area and a partial separation of the samples of the Rax area at the one and the samples of the Hohe Wand and the Wienerwald area at the other side. Also these distribution areas of the samples are overlapping at a high degree.

Scatter plots of regression factor 1 and 2 of all samples including the SMF specimens based on three morphologically important measures (Fig. 11) discloses a remarkable morphological isolation of some SMF specimens, especially of those specimens assigned to *Clausilia dubia speciosa, C. d. dubia, C. d. floningiana* and *C. d. floningiana/gracilor, C. d. graci-*

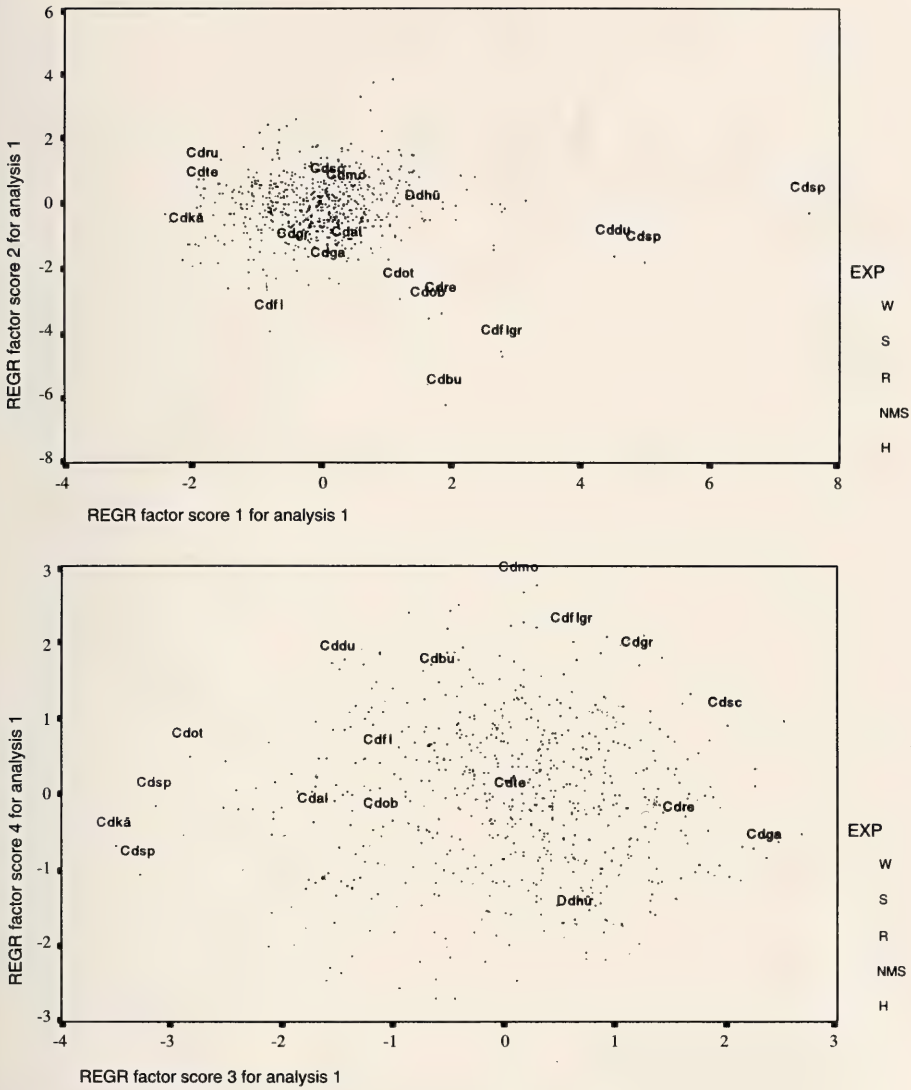


Figure 11. Scatter plots of the samples and the NMS specimens with value 1 and 2, 3 and 4 (points represent samples, NMS specimens with abbreviations).
Figura 11. Diagramas de puntos de las muestras y los especímenes NMS con valores 1 y 2, 3 y 4 (los puntos representan las muestras, los especímenes NMS son las abreviaturas).

lior, C. d. grimmeri, and also C. d. bucculenta. These specimens are found outside the central area of distribution of the two dimensional coordinate system of the scatter plot, where the bulk of specimens appears in a high concentration.

A scatter plot of the factors 3 and 4 (Fig. 11) shows us more peripheral positions of *Clausilia dubia moldanubica, C. d. otvinensis, C. d. speciosa, C. d. kaeufeli, C. d. gracilior, C. d. schlechti, C. d. grimmeri* and *C. d. floningiana/gracilior*.

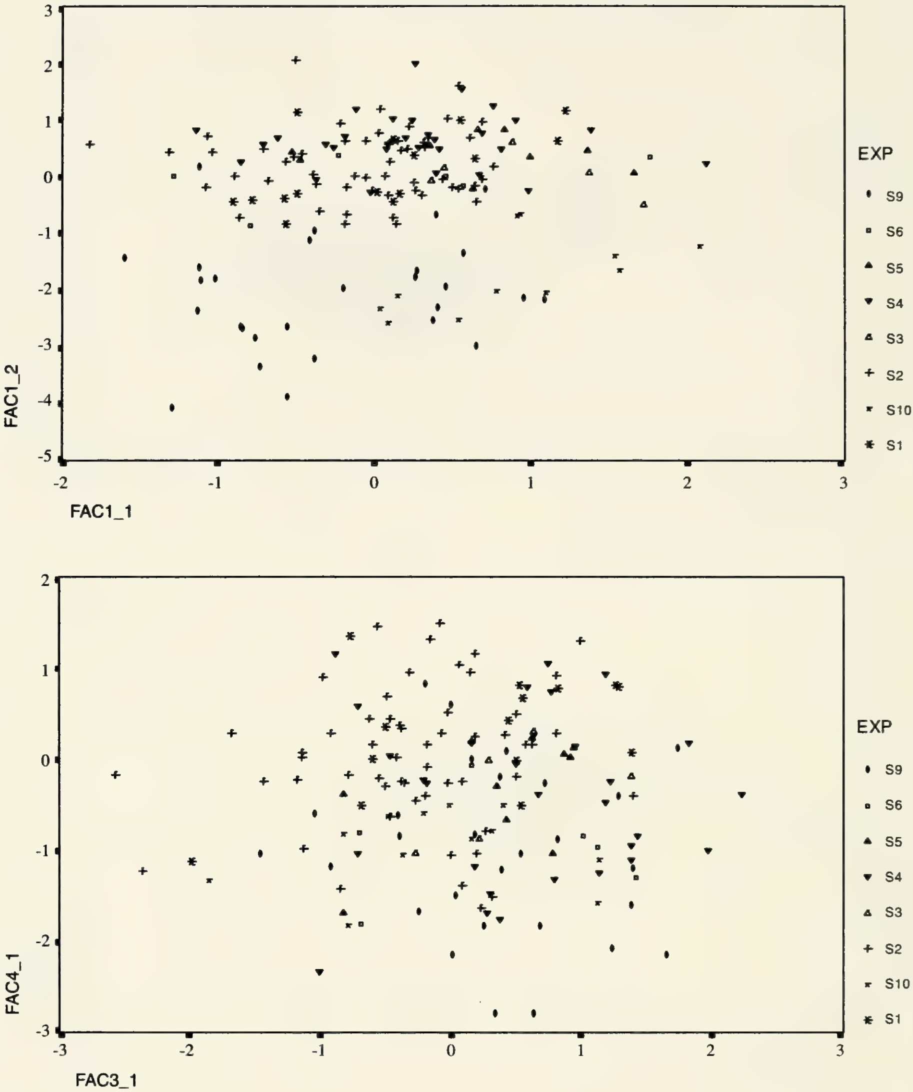


Figure 12. Two-dimensional scatter plots with factors 1/2 and 3/4 of a spot check of the Schneeberg samples (see the altitude of the sample areas at Material and methods).
Figura 12. Diagramas de puntos de dos dimensiones con factores 1/2 y 3/4 de las muestras de Schneeberg (ver la altitud de las áreas de muestreo en Material y métodos).

Scatter plots of the factors 1 to 4 of the various samples of the Schneeberg area (from different altitudes) disclose no remarkable dependence of the factors 1, 3 and 4 on altitude (Fig. 12).

Factor 2 shows us a separate distribution of values of sample S9 (1850 m) and S10 (1650 m). The distribution areas of the other samples are covering one another. They are overlapping distribution areas of sample S9 and S10 insignificantly.

A scatter plot of the Rax samples (Fig. 13) which were arranged in correspondence to the altitude in three groups

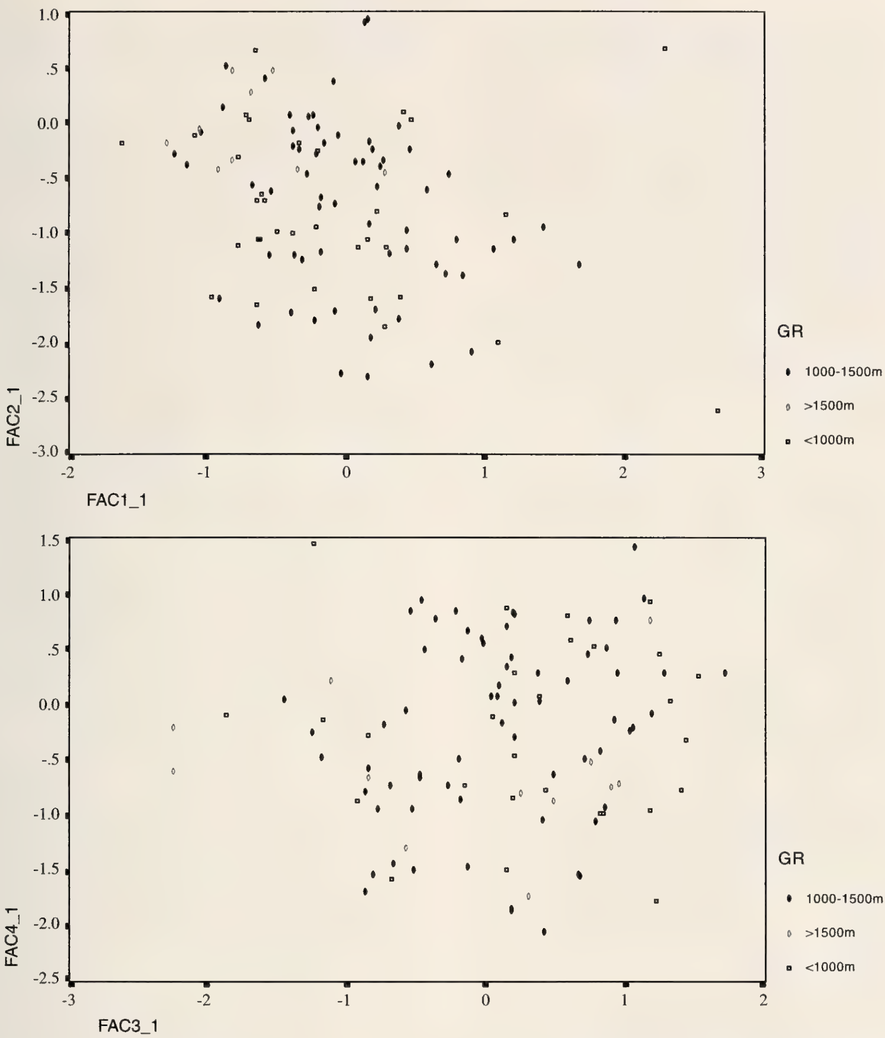


Figure 13. Two-dimensional scatter plots with factors 1/2 and 3/4 of a spot check of the Rax samples, arranged in three groups in accordance with the altitude of the sample areas (less 1000 m, 1000-1500 m, more than 1500 m).

Figura 13. Diagramas de puntos de dos dimensiones con factores 1/2 y 3/4 de las muestras de Rax , ordenadas en tres grupos de acuerdo con la altitud de las áreas de muestreo (menos de 1000 m, 100-1500 m, más de 1500 m).

(less than 1000m, 100-1500m, more than 1500m) results no altitude dependence of the factors.

Cluster analysis: For the first cluster analysis the measured values were taken from a group of specimens which consisted of selected samples from different localities and altitudes; data from the SMF specimens were also included (Fig. 14). The hierarchical cluster which is presented as a dendrogram contains groups of different size which were collected at different localities.

Notable is the isolated position of the SMF specimens of *Clausilia dubia speciosa* and *C. d. dubia* which constitute a cluster of their own together with two specimens of the samples. Almost the same phenomena occur in dendrograms of samples collected in the areas "Hohe Wand", "Schneeberg" and "Rax". In these cases specimens of the SMF were also taken into consideration.

In general the clusters show remarkable segregations. Similarities of the individuals coming out from the same locality and appearing together in clusters may be seen as indication of close relationship.

At the other side the spot checks from various areas are overlapping at a high degree. Relevant portions of individuals, which present all the characters of several "subspecies" (subspecies seen in the traditional way) do not occur. It is remarkable that most specimens from the SMF which were considered to be typical for specific regions, appear also in the different branches of the dendrograms and in various clusters.

Only the SMF specimens of *Clausilia dubia speciosa*, and in a most astonishing way, the SMF specimen of *C. d. dubia*, an individual belonging to the nominotypical subspecies" are seen at own separate branches of the dendrograms. This finding is in full agreement with the above mentioned scatter plots of the analysis of the main components. All three above mentioned specimens are characterized by strongly deviating measures and stand in isolated positions. It is evident that this finding disagrees with the geographical distribution shown in the literature (KLEMM, 1960).

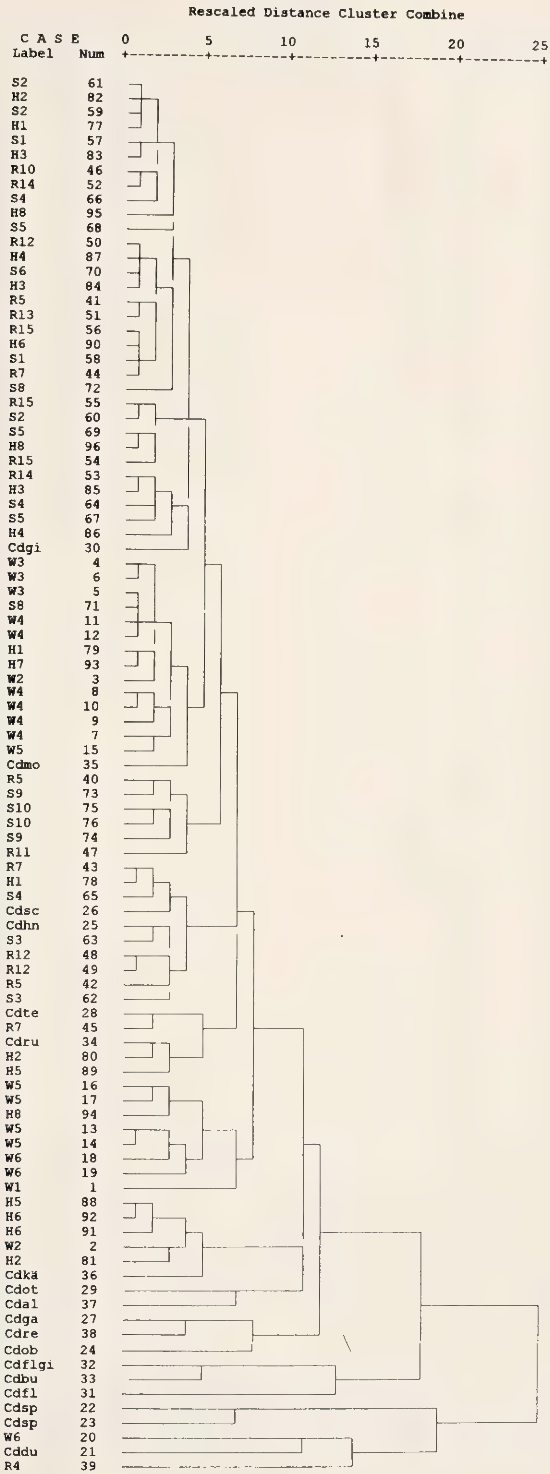
Wienerwald: The samples from the Wienerwald area come from altitudes between 270 and 400 m and sites similar in climate and ecological conditions (fir, pine, and mixed forests).

The shells are rather similar and club shaped, but differ considerably in shell height and width, height and width of aperture, and distance of ribs. The same is true for all the other measures taken. In the hierarchical cluster analysis of samples from the Wienerwald area (Fig. 15) which was considered to be the type locality of *Clausilia dubia dubia*, the position of *C. d. dubia*, *C. d. kaeufeli*, and *C. d. speciosa* is found to be extremely isolated in a cluster of their own (Fig. 16). Within the second cluster also other SMF specimens appear in entirely isolated branches. Only *C. d. runensis*, *C. d. tettelbachiana*, *C. d. grimmeri*, *C. d. schlechti* and *C. d. moldanubica* appear in a branch together with the specimens of the samples from the Wienerwald area.

Hohe Wand: Analyses of samples taken from the Hohe Wand (altitude between 560 m and 1080 m; Fig. 16) also lead to results which are not in accordance with generally held views. *Clausilia dubia speciosa* and *C. d. runensis* are in an isolated position. They are in a cluster of their own together with one specimen of the local sample from H8. Also *C. d. bucculenta*, *C. d. floningiana/gracilior*, *C. d. floningiana*, *C. d. reticulata*, *C. d. obsoleta*, *C. d. gracilior*, *C. d.*

(Right page). Figure 14. Hierarchical cluster of a spot-check of all samples and the SMF specimens (Wi-y= specimens of the Wienerwald area; i= sample; y= number of the specimen; Hi-y= specimens of the Hohe Wand area; Si-y= specimens of the Schneeberg area; Ri-y= specimens of the Rax area; Cd-= specimens of the SMF: du= *dubia*; sp= *speciosa*; ob= *obsoleta*; hn= *huettneri*; sc= *schlechti*; gr= *gracilior*; te= *tettelbachiana*; ot= *otvinensis*; gi= *grimmeri*; fl= *floningiana*; flgr= *floningiana/gracilio*r; bu= *bucculenta*; ru= *runensis*; mo= *moldanubica*; kä= *kaeufeli*; al= *alpicola*; re= *reticulata*).

(Página derecha). Figura 14. Cluster de todas las muestras y los especímenes SMF (Wi-y= especímenes del área de Wienerwald; i= muestra; y= número del especimen; Hi-y= especímenes del área de Wand; Si-y= especímenes del área de Schneeberg; Ri-y= especímenes del área de Rax; Cd-= especímenes SMF: du= dubia*; sp=* speciosa*; ob=* obsoleta*; hn=* huettneri*; sc=* schlechti*; gr=* gracilior*; te=* tettelbachiana*; ot=* otvinensis*; gi=* grimmeri*; fl=* floningiana*; flgr=* floningiana/gracilior*; bu=* bucculenta*; ru=* runensis*; mo=* moldanubica*; kä=* kaeufeli*; al=* alpicola*; re=* reticulata*).*


Rescaled Distance Cluster Combine
C A S E
Label Num
0 5 10 15 20 25
S2 61
H2 82
S2 59
H1 77
S1 57
H3 83
R10 46
R14 52
S4 66
H8 95
S5 68
R12 50
H4 87
S6 70
H3 84
R5 41
R13 51
R15 56
H6 90
S1 58
R7 44
S8 72
R15 55
S2 60
S5 69
H8 96
R15 54
R14 53
H3 85
S4 64
S5 67
H4 86
Cdgi 30
W3 4
W3 6
W3 5
S8 71
W4 11
W4 12
H1 79
H7 93
W2 3
W4 8
W4 10
W4 9
W4 7
W5 15
Cdmo 35
R5 40
S9 73
S10 75
S10 76
S9 74
R11 47
R7 43
H1 78
S4 65
Cdsc 26
Cdhn 25
S3 63
R12 48
R12 49
R5 42
S3 62
Cdte 28
R7 45
Cdru 34
H2 80
H5 89
W5 16
W5 17
H8 94
W5 13
W5 14
W6 18
W6 19
W1 1
H5 88
H6 92
H6 91
W2 2
H2 81
Cdkä 36
Cdot 29
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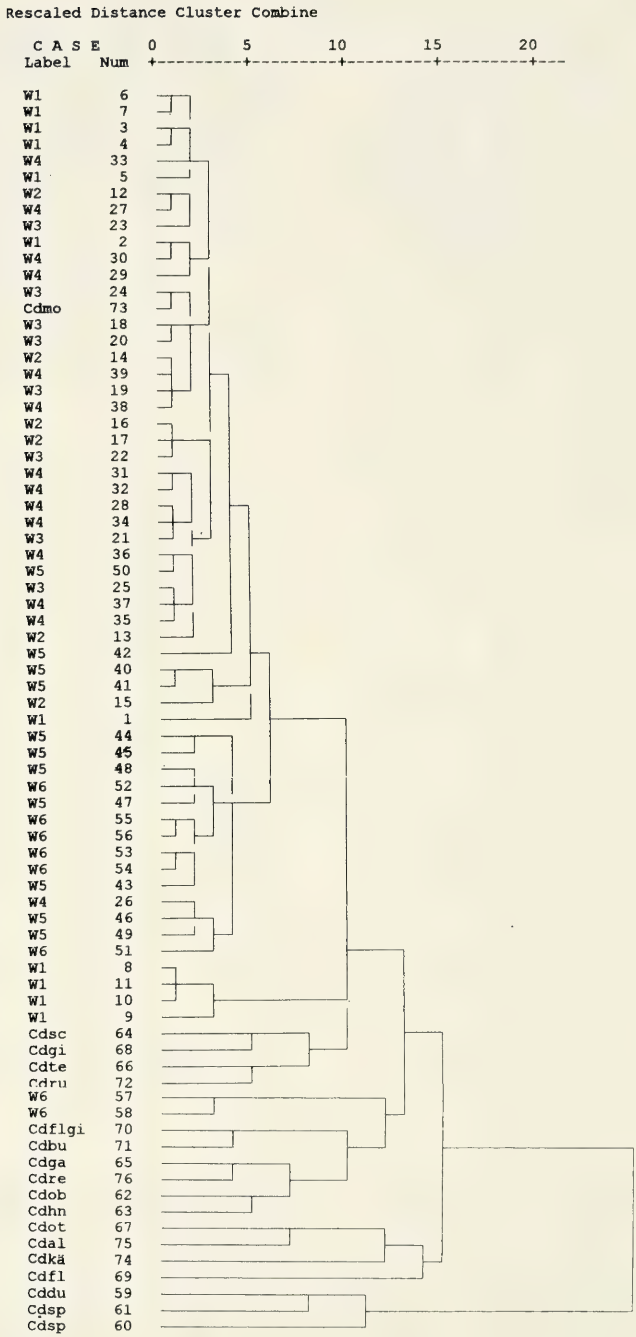

Figure 15. Hierarchical cluster of a spot check of all samples of the Wienerwald area and the SMF specimens. Abbreviations as in Figure 14.

Figura 15. Cluster de todas las muestras del área de Wienerwald y los especímenes SMF. Abreviaturas como en la Figura 14.

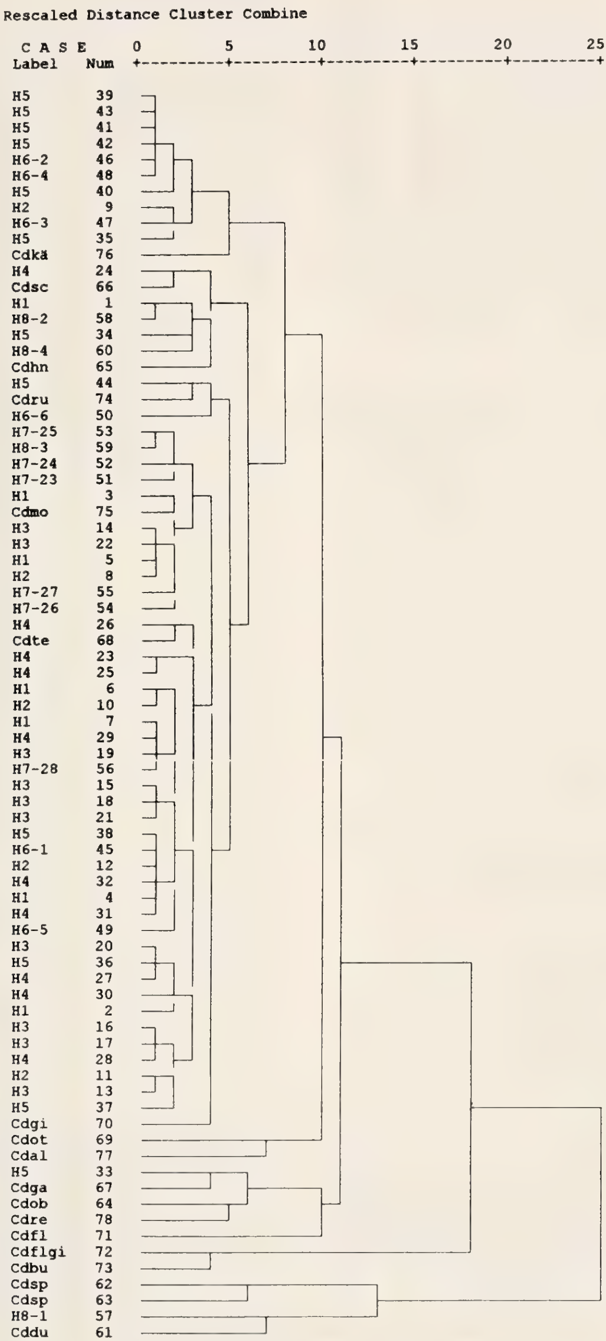

Figure 16. Hierarchical cluster of a spot check of all samples of the Hohe Wand area and the SMF specimens. Abbreviations as in Figure 14.

Figura 16. Cluster de todas las muestras del área de Hohe Wand y los especímenes SMF. Abreviaturas como en la Figura 14.

alpicola, C. d. otvinensis and *C. d. grimmeri* occur in separated branches and only *C. d. tettelbachiana, C. d. moldanubica, C. d. huettneri* and *C. d. kaeufeli* are integrated in branches together with the major part of the specimens from the Hohe Wand area. There are no indications of the succession postulated by former workers (KLEMM, 1960) when one takes into consideration altitudes of the localities from which they came and the similarities that appear in the dendrogram.

Schneeberg: The studied material was collected at altitudes between 700 to 1850 m. The cluster analysis (Fig. 17) reveals morphologically isolated positions for *Clausilia dubia speciosa, C. d. dubia, C. d. kaeufeli, C. d. floningiana, C. d. reticulata, C. d. obsoleta, C. d. bucculenta, C. d. floningiana/gracilior, C. d. alpicola, C. d. otvinensis, C. d. tettelbachiana, C. d. runensis* and *C. d. moldanubica*. Only *C. d. grimmeri, C. d. gracilior* and *C. d. schlechti* occur in branches together with most of the specimens of the Schneeberg spot checks. Remarkable is that specimens with close morphological relations to *C. d. kaeufeli*, as expected for the peak of the mountain, don't occur in the clusters. The SMF specimen of *C. d. kaeufeli* is isolated in the dendrogram.

Rax: The studied material was collected at altitudes between 700 to 1685 m. As in the Clusters analyses of the other areas *Clausilia dubia dubia*, and *C. d. speciosa* are isolated in a Cluster of ist own (Fig. 18). Also *C. d. kaeufeli, C. d. floningiana, C. d. bucculenta, C. d. floningiana/gracilior, C. d. runensis, C. d. alpicola, C. d. otvinensis, C. d. otvinensis, C. d. obsoleta, C. d. reticulata* and *C. d. gracilior* occur very isolated in branches together with only few specimens of the local samples. Only *C. d. grimmeri, C. d. moldanubica, C. d. tettelbachiana, C. d. schlechti* and *C. d. huettneri* can be seen as well integrated in clusters with the major part of the local samples. No remarkable position of *C. d. kaeufeli* or a succession as suggested by Klemm was visible.

DISCUSSION AND CONCLUSION

The conclusions presented here must be seen as being valid only for samples of *Clausilia dubia* collected in restricted areas. Only further research might lead to conclusive results on possible geographic variation in *C. dubia*.

The results of the present research as well as a critical evaluation of those of earlier researchers show us the limits inherent the intuitive, subjective method used in the analysis of characters. Earlier studies by EDLINGER AND MILDNER (1979) on *Clausilia dubia* in *Carinthia*, using traditional morphological methods based on a number of shell characters, also showed a high variability of most of these characters within each population. This may be a common phenomenon when analyses are based on a large number of characters. In this case, techniques of measurement, as well as applied statistical methods might present potential sources of error.

Nevertheless, all observations are indicative of high variability within the species. Similar observations can be made in many of the collection samples (Fig. 6). This can be clearly discerned, in spite of the fact that many of these samples have been classified as belonging to various subspecies.

To gain a better understanding of shell variability, we must also consider the influence of ecological factors, and the life history of the specimens. Morphological features may be influenced by non hereditary factors too (GOODFRIEND, 1986).

Against the background of low correlation coefficients between altitude and most characters, except columellar lamella, altitude in itself cannot be conceived as an substantial ecological factor, because the measures of the shells except the columellar lamella don't vary significantly in correlation with altitude. A reason for the remarkable correlation of altitude with the columellar lamella might be that the *Clausilia dubia* shells of the Wienerwald area commonly have very pregnant incisions of the columellar lamella.

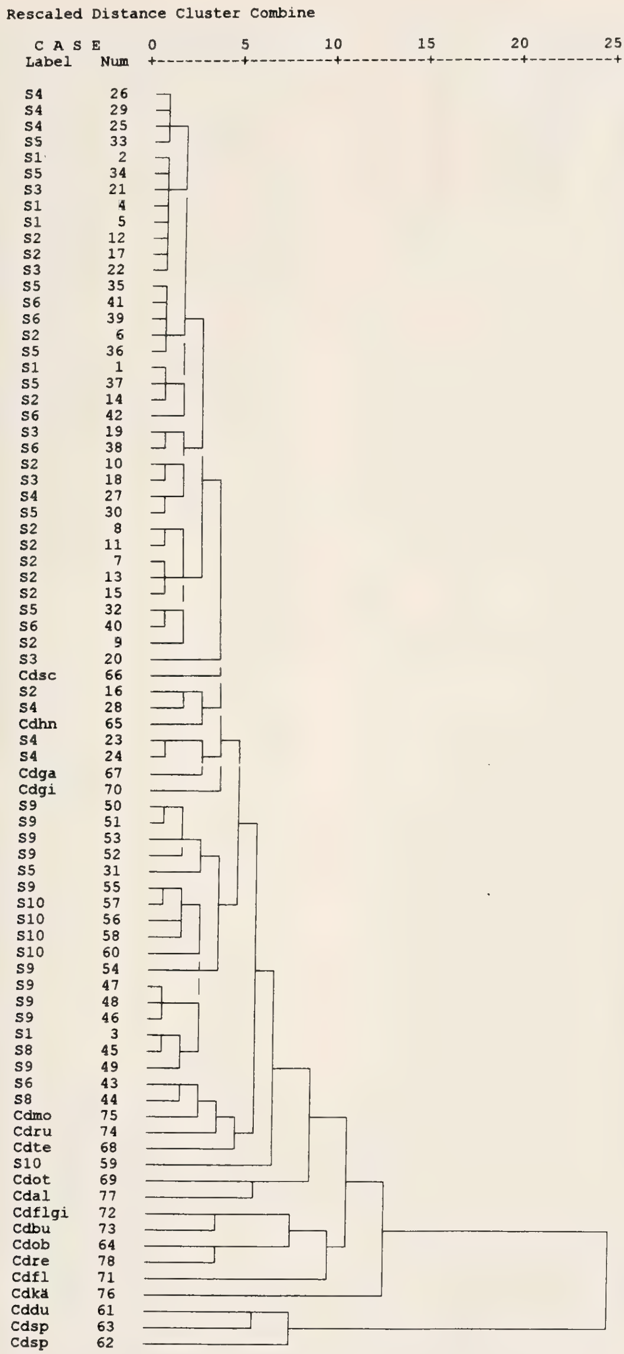

Figure 17. Hierarchical cluster of a spot check of all samples of the Schneeberg area and the SMF specimens. Abbreviations as in Figure 14.
Figura 17. Cluster de todas las muestras del área de Schneeberg y los especímenes SMF. Abreviaturas como en la Figura 14.

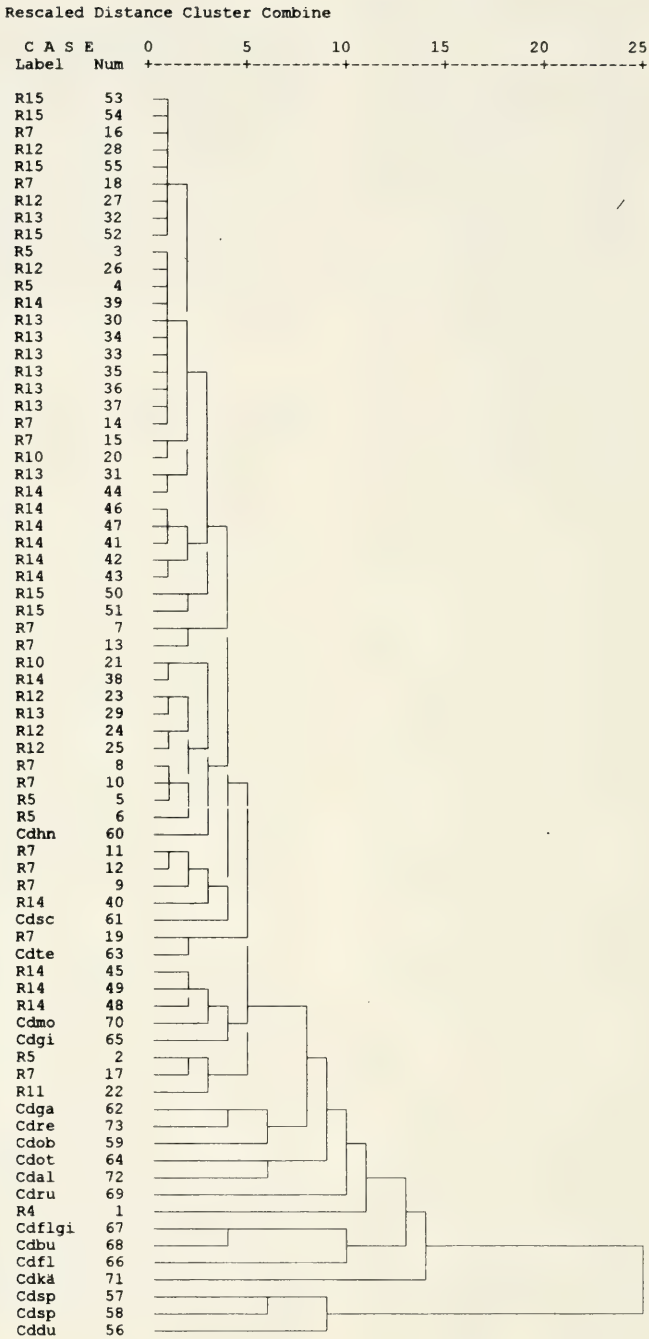

Figure 18. Hierarchical cluster of a spot check of all samples of the Rax area and the SMF specimens. Abbreviations as in Figure 14.

Figura 18. Cluster de todas las muestras del área de Rax y los especímenes SMF. Abreviaturas como en la Figura 14.

Other ecological factors may be of relevance, but we must consider them as arranged in ensembles and affecting upon animals collectively.

Certainly, individual living conditions, as well as hereditary dispositions, result in specific modifications of characters. nevertheless we can reject the hypothesis of EDLINGER AND MILDNER (1982) that the characteristics of *Clausilia dubia runensis* might be a result of helminth parasitism.

A representation of variability of species or populations by character analysis also has to take into consideration the fact that many characters act as correlated variables. In these cases one can speak of character complexes. Arrangements in complexes restrict variability. The question arises, whether there are other factors influencing the variables mentioned above, which are not subjects of the researches presented above. Shells, for example, function as hard skeletons and as mechanical abutments for musculature. Hard skeleton and musculature must be suited to each other. So it is evident, that morphological relations between various measures of the shell are indirectly caused by constructional needs of the animal as a whole and also of the soft body in particular (GUTMANN, 1989; EDLINGER, 1991).

Considering the local patterns of distribution of values and primary components inside the species and its populations, these patterns must be seen as varying locally and gradually. The variation of patterns must be seen as the result of local variation, following from step by step changes of frequencies of characters. When different frequencies are developed under similar ecological conditions, we may assume that these changes are a result of genetic drift.

Certain local accumulation of special characters resp. values of variables may result from genetic drift too. Typical characters of the so called *"Clausilia dubia runensis"*, *C. d. speciosa* (shell form) or *"C. d. otvinensis"* (distances between shell ribs), for example, occur in separate areas with large distances between them. Other characters of the same animals very often don't differ from that of surrounding populations in adjacent areas (EDLINGER AND FISCHER, 1997).

This leads us to the conclusion that frequencies of special characters cannot automatically be taken as a reason for a common origin of separated populations resp. of a heterogeneous origin of contiguous populations. Above all this is true, when other characters are identical with those of contiguous populations.

So it may be that genetic drift or special environmental factors have an influence on single characters. With regard to these characters we may conceive of some populations as homogenous and "pure bred". At the other side there cannot arise populations being homogeneous and "pure bred" in all or most characters and containing such a high number of "typical specimens" homogenous in most or in all characters by simple environmental influences.

In any case, "typical" or "pure bred" specimens were recognized mostly by earlier researchers, and are extremely arbitrary. So, the natural populations of *Clausilia dubia* which were investigated do not match the preconceived expectations of well established races or subspecies occurring in well delimited areas with rare interbreeding occurrences. Therefore, we must question, if a morphologically uniform population of *Clausilia dubia* which can be defined as a subspecies or race, might ever have existed in the eastern Alpine region.

KLEMM (1960) who was of the same opinion, believed that the transitional stages between the races and subspecies might be the consequence of (post glacial) re-immigration of pure bred populations, and their subsequent mixing with other local forms.

Shell characters, and their distribution patterns do not support this hypothesis. Additionally, cluster analysis shows that very variable samples come from regions where the forerunners of present populations must definitely have lived and survived during the Pleistocene. Contrary to KLEMM (1960), we must state that a reconstruction of

events after the Pleistocene gives us no evidence to support this view. Why should areas, glaciated during the Pleistocene be resettled by the descendants of single, pure bred populations after the disappearance of the ice?

A new interpretation of character distribution seems to be more adequate for the case presented, and discussed here. This interpretation requires the (for the case discussed here) use of theorems which are accepted by most anthropologists (CAVALLI-SFORZA, MENOZZI AND PIAZZA, 1994; KLEIN, TAKAHATA AND AYALA, 1994).

According to their theoretical guidelines, the definition of subspecies and race depends on subjective argumentations, and does not mirror objective, concrete facts. They also accept diversity within given populations. Therefore, distribution and frequency of characters are subject to constant change.

Thus, in any investigated snail population, only the distributions of characters, and the frequency of their occurrence can be reasonably recorded. This entirely altered interpretation also corresponds better with the results of genetic analysis in various species of *Albinaria* (MYLONAS, KRIMBAS, TSIAKAS AND AYOUNTANTI, 1990; SCHILTHUIZEN, 1994). The results of these studies show that there is an overlap of genetic features in some of the traditionally recognized subspecies, and even of species. Similar results may be expected for *Clausilia dubia*.

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Dendrodoris limbata **(Cuvier, 1804)**
Sinonimias
Doris limbata Cuvier, 1804, *Ann. Mus. H. N. Paris*, 4 (24): 468-469 [Localidad tipo: Marsella].
Doris nigricans Otto, 1823, *Nov. Act. Ac. Caes. Leop. Car.*, 10: 275.

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Synonyms

Doris limbata Cuvier, 1804, *Ann. Mus. H. N. Paris*, 4 (24): 468-469 [Type locality: Marseille].

Doris nigricans Otto, 1823, *Nov. Act. Ac. Caes. Leop. Car.*, 10: 275.

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Only Latin words and names of genera and species should be underlined once or be given in *italics*. No word must be written in UPPER CASE LETTERS. SI units are to be used, together with their appropriate symbols. In Spanish manuscripts, decimal numbers must be separated with a comma (,), NEVER with a point (.) or upper comma (').

• References in the text should be written in small letters or SMALL CAPITALS: Fretter & Graham (1962) or FRETTER & GRAHAM (1962). The first mention in the text of a paper with more than two authors must include all of them [Smith, Jones & Brown (1970)], thereafter use *et al.* [Smith *et al.* (1970)]. If an author has published more than one paper per year, refer to them with letters: (Davis, 1989a; Davis, 1989b). Avoid *op. cit.*

The references in the reference list should be in alphabetical order and include all the publications cited in the text but only these. ALL the authors of a paper must be included. These should be written in small letters or SMALL CAPITALS. The references need not be cited when the author and date are given only as authority for a taxonomic name. Titles of periodicals must be given IN FULL, not abbreviated. For books, give the title, name of publisher, place of publication, indication of edition if not the first and total number of pages. Keep references to doctoral theses or any other unpublished documents to an absolute minimum. See the following examples (please note the punctuation):

Fretter, V. and Graham, A., 1962. *British Prosobranch Molluscs.* Ray Society, London, 765 pp.

Ponder, W. F., 1988. The Truncatelloidean (= Rissoacean) radiation - a preliminary phylogeny. In Ponder, W. F. (Ed.): Prosobranch Phylogeny, *Malacological Review*, suppl. 4: 129-166.

Ros, J., 1976. Catálogo provisional de los Opistobranquios (Gastropoda: Euthyneura) de las costas ibéricas. *Miscelánea Zoológica*, 3 (5): 21-51.

• Figures must be original, in Indian ink on draughtsman's tracing paper. Keep in mind page format and column size when designing figures. These should be one column (57 mm) or two columns (120 mm) wide and up 194 mm high, or be proportional to these sizes. Two columns format is recomended. It is desirable to print figures with their legend below, so authors are asked to take this into account when preparing full page figures. If computer generated graphics are to be included, they must be printed on high quality white paper with a laser printer. Photographs must be of good contrast, and should be submitted in the final size. When mounting photographs in a block, ensure spacers are of uniform width. Remember that grouping photographs of varied contrast results in poor reproduction. Take account of necessary reduction in lettering drawings; final lettering must be at least 2 mm high. In composite drawings, each figure should be given a capital letter; additional lettering should be in lower-case letters. A scale line is recomended to indicate size, magnification ratio must be avoided as it may be changed during printing. UTM maps are to be used if necessary. Figures must be submitted on separate sheets, and numbered with consecutive Arabic numbers (1, 2, 3,...), without separating 'Plates' and 'Figures'. Legends for Figures must be typed in numerical order on a separate sheet, and an English translation must be included. Follow this example (please note the punctuation):

Figure 1. *Neodoris carvi.* A: animal crawling; B: rinophore; C: gills.

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Junta directiva desde el 18 de octubre de 1996

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